The Use of Catch-Effort and Tagging Data in Estimating a Flatfish Population

By K. S. Ketchen
Pacific Biological Station, Nanaimo, B.C.

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ABSTRACT

By a modification of the DeLury method an estimate is made of the stock of lemon sole (*Parophrys vetulus*) on the fishing grounds in Hecate Strait, British Columbia. The method is based on (1) the trend in catch of tagged fish per unit of effort in relation to accumulated catch of tagged fish, and (2) the trend in catch of untagged fish per unit of effort in relation to accumulated catch of untagged fish. At the start of the experiment 4.72 million pounds are estimated to have been present, while during the experiment 3.74 million pounds entered the area of fishing, 3.26 million pounds emigrated from it, and 2.54 million pounds were caught.

A Petersen-type estimate based on the ratio of tagged to untagged fish was 4.70 million pounds present at the start of the experiment—practically identical with the one derived from catch-effort information. Total population for the year (1950) is estimated as 9.8-12.2 million pounds, including catch and possible emigration prior to the experiment, the stock on the fishing grounds at the start of the experiment, and the immigration subsequently.

The average annual survival rate of age VII – age IX lemon soles in Hecate Strait has decreased from 0.770 to 0.614 during the period of growth of the fishery, 1944-1951. From this difference the average rate of exploitation is estimated as 16 to 20 per cent and the average population as 8.9 to 11.5 million pounds. Since this range is nearly the same as the range described above, it is concluded that almost the whole of the Hecate Strait stock was accessible to fishing in 1950, which was a year of unusually high production.

INTRODUCTION

The estimation of the size of fish populations by means of the release and recapture of tagged individuals has been practised widely since the turn of the century. Various modifications in the method have yielded estimates either from the ratio in the catches of tagged and untagged fish or from information on the rate of recovery. Tagging estimates, however, entail a great variety of assumptions which, particularly in marine populations, are not only difficult to test but are apt to be so much in error as to limit seriously the validity of the results. Procedures have been developed recently by DeLury (1947, 1951) to obtain estimates of population size from information on catch and the trend in catch per unit of effort. As the results are independent of those obtained from tagging, they afford a much-needed check on tagging estimates.

The purpose of this paper is (1) to compare the estimates of a population of flatfish as obtained through the use of information on catch-effort and tag recoveries, (2) to demonstrate how the DeLury method may be extended with the aid of tagging data to account effectively for immigration and emigration,

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and (3) to use the results of this extension in company with data on catch and rate of exploitation to compute the total stock of fish.

Recent attempts to estimate a flatfish population on the basis of the decline in catch per unit of effort as related to fishing effort have been recorded by Kawasaki and Hatanaka (1951).

ACKNOWLEDGMENTS

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Catch records of United States trawlers have been made available to the author through the kind co-operation of the Washington State Department of Fisheries.

BIOLOGICAL BACKGROUND

The flatfish species which will be the subject of study is the lemon "sole", *Parophrys vetulus*, one of fifteen members of the flounder family which occur off the British Columbia Coast. Attention will be given to a population which inhabits Hecate Strait, that body of water lying between the Queen Charlotte Islands and the mainland of the Province.

Until the middle of World War II the fishery for lemon soles in Hecate Strait was virtually nonexistent. In the past seven years (1945-51) the catch and catch per unit of effort (Table I) during the spring months has fluctuated

TABLE I. The known catch and seasonal availability of lemon soles in Hecate Strait (1942–1951).

Year	Catch in millions of pounds		Total catch	Availability (pounds per hour)
	Canadian	American		
1942	(0.1)[a]	.....	(0.1)	?
1943	(0.3)	.....	(0.3)	?
1944	(0.6)	.....	(0.6)	?
1945	0.7	?	?	1200
1946	1.1	?	?	820
1947	0.3	?	?	850
1948	1.5	0.4	1.9	680
1949	0.7	1.1	1.8	590
1950	3.5	0.9	4.4	1210
1951	1.2	0.8	2.0	750

[a]Brackets indicate estimated catch.

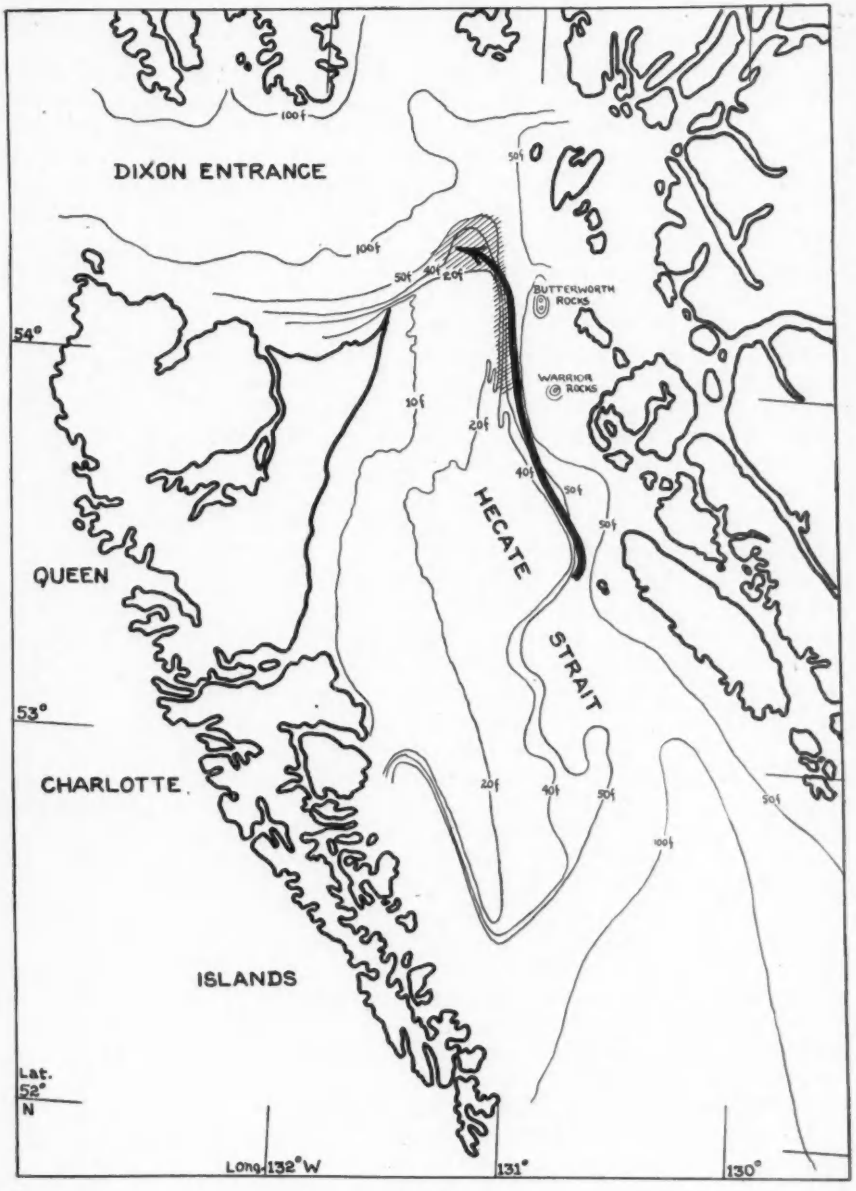

FIGURE 1. The location in Hecate Strait of the fishery for lemon soles (shaded area) and the migration route during the spring months (heavy arrow).

considerably because of variations in the amount of effort expended and variations in the vulnerability of the fish to capture. The experiment which is to be described took place during the spring of 1950, a year when the catch and availability (catch per unit of effort) were unusally high.

Fishing is carried out by Canadian and United States trawlers operating along a 25-mile "edge" of the Hecate Strait bank which projects eastward from the shores of the Queen Charlotte Islands. During the brief period in which the lemon sole population is available each year (late winter and spring) it is known to move northward along this "edge" in the direction of Dixon Entrance (Figure 1). Although some individuals or schools appear to pass through the fishing area fairly quickly (perhaps within one week) the main movement is slow, taking 10 to 15 weeks to complete.

The starting point of the migration is unknown. Since the fish are in a spent condition when they appear on the trawlable grounds, they are presumed to be moving from a winter spawning area somewhere in the southern part of the strait. During the summer months they become dispersed along the northwestern edge of the Hecate Strait bank where it projects into Dixon Entrance. A more detailed account of the migration is given elsewhere (Ketchen, 1950).

The ages of the lemon soles which are caught by the commercial fleet range from four to fourteen years, with the average occurring usually from five to seven. The age and length composition of the catches within the area of study are reasonably homogeneous throughout the season. Any lack of homogeneity is usually attributed to variations in sex ratio. The male lemon sole is much smaller than the female and is therefore subjected to more severe culling. There is no apparent trend in size or sex ratio throughout the season of availability.

Manzer (1951) has shown from tagging studies that the Hecate Strait lemon sole completes about 30 per cent of its annual growth in length by the end of April, and roughly 70 per cent by the end of June. Since the average size of lemon soles taken during the course of the experiment was 370 mm. and since fish of this size may be expected to grow 11 mm. in one year, the growth during the period of study (eight weeks beginning on April 29 and ending June 22) was 4 mm. The increase in weight corresponding to this length increase would be 0.56 oz. (16 g.) or 3,500 pounds per hundred thousand fish.

From the age composition of the essentially virgin stock of 1944 and 1945 the natural mortality rate has been estimated to be approximately 23 per cent per annum. Thus, presuming that mortality occurs at a uniform rate throughout the year, the rate during this period of study would be about 3.5 per cent.

CATCH-EFFORT DATA

Most of the Canadian catches of flatfish from the Hecate Strait bank are landed at the port of Prince Rupert. The remainder are landed at Vancouver or Victoria or at the small middle-coast ports of Klemtu and Namu. At the ports of Prince Rupert, Vancouver and Victoria the Pacific Biological Station maintains observers who contact the skipper of each vessel as he lands his catch.

Information is collected on the date of landing, the area of fishing, the number of days absent from port, the number of days spent in fishing, the average number of hours of fishing each day and the total catch of each species. This information is the basis for computing the catch per unit of effort.

Records of catches landed at United States ports and at Canadian ports not covered by port observers have no effort assigned to them and hence are useful only for consideration of total catch. Such records constituted approximately 25 per cent of the landings.

In order to obtain a day-to-day record of the catch and effort from boats contacted it has been necessary to break down the catch of each trip according to the number of days fishing. Knowing the date of landing, the number of days absent, the number of days fishing, and the wind conditions during the period of absence (as obtained from lighthouse meteorological records), it has been possible to estimate fairly closely the actual dates when the catches were made during each trip. To these dates the catch and effort have been apportioned equally.

When more than one species occurs on a particular fishing bank at any given time, it is usually difficult to assign to individual species the effort expended in fishing. The experienced fisherman is capable of controlling the proportions of the various species in his catch, simply by his selection of locality, type of bottom, and depth, and by modification of the operation of his net. Ordinarily, in computing the catch per unit of effort for lemon soles, only those records are used in which at least 50 per cent of the total catch for a trip is composed of that species. It so happened, however, that during the period of study, the lemon sole dominated the catches throughout, thus obviating the need for making adjustments for the "species factor".

To compensate for differences in gear efficiency among boats, a "boat factor" has been computed for each of the 35 Canadian vessels which participated in the fishery. A "period factor" also has been introduced to account for the effects of boats which did not fish during the entire period of study. The weighted catches for all boats have been summed for each day and divided by the number of hours of effort to give a weighted catch per unit of effort for each day.

TAGGING DATA

The lemon soles used in the tagging experiment were caught by the research trawler *Investigator No. 1* which operated along with the fishing fleet in Hecate Strait. Each fish was marked by the attachment of a Petersen-type disc tag to the dorsal part of the body.

On April 7, 1950, a total of 823 tagged fish were released at the southern end of the fishing ground adjacent to the Warrior Rocks (Figure 1). A second tagging conducted on April 23 and 24 adjacent to the Warrior Rocks and adjacent to the Butterworth Rocks involved a total of 2,180 fish. A summary of the tag recovery during the 1950 fishing season appears in tabular form in Appendix I.

When a tagged fish is recaptured the fisherman turns it over to the Pacific Biological Station's representative at whichever port he lands. In order to make the tag-recovery records comparable to the catch-effort records, it has been necessary to assign the recoveries to days of active fishing (few fishermen bother to report the actual date of recovery of tagged fish). The procedure followed for distributing the tag recoveries in accordance with the dates of fishable weather was the same as that used in assigning the catch and effort to individual days.

CALCULATIONS

(1) Catch-Effort Estimates

Using De Lury's symbols, the catch during a given time interval t is denoted as $c(t)$ and the effort expended in making the catch is denoted as $e(t)$. The catch per unit of effort for interval t is then $C(t) = c(t)/e(t)$. As a basis for his demonstration of the relation of $C(t)$ to the population size, DeLury makes three assumptions about the population: (1) that it is closed, (2) that the units of effort do not compete with one another, and (3) that the *catchability*, k (that fraction of the population captured by one unit of effort), is constant.

Under these assumptions DeLury has demonstrated that the following relation holds:

$$C(t) = kN(o) - kK(t), \qquad (I)$$

where $K(t)$ represents the total catch up to, but not including, time t. $N(o)$ and $N(t)$ represent the number of individuals in the initial population and in the population at any time t. If the line relating $C(t)$ to $K(t)$ is acceptably straight, then values may be computed for k and $N(o)$. Significant curvature in the graph would indicate that the assumptions are in need of some modification.

When the catch per unit of effort decreases to zero the entire population theoretically has been captured and the accumulated catch to that time will represent the population. Hence, a graphical estimate of $N(o)$ may be obtained by extrapolating the line to the $K(t)$ axis. This relationship is illustrated by say line AF in Figure 2.

In a population where the three assumptions of DeLury are satisfied the slope of the line will be dependent on the effectiveness of fishing and hence will be a measure of k, the true catchability of the population. In a population which is not closed, there may be (1) immigration only, (2) emigration only, or (3) both immigration and emigration. In all three cases the slope of the line relating catch per unit of effort to catch would yield k_a, the *apparent catchability* of the population. Only if immigration is continuously balanced by emigration would $k_a = k$, the true catchability.

If fish were emigrating from the area of fishing at a rate proportional to the stock on hand, then the graph would assume some position AH with a slope greater than that of AF. Such a condition is described by DeLury's (1951) equation,

$$C(t) = kN(o) - \left(k + k'\frac{e'}{e}\right) K(t), \qquad (II)$$

where two processes operate simultaneously to reduce the stock. In this case e and k might be associated with fishing and e' and k' with emigration. If emigration occurred not in proportion to the stock on hand but at some constant absolute rate then line AH would tend to be concave downwards.

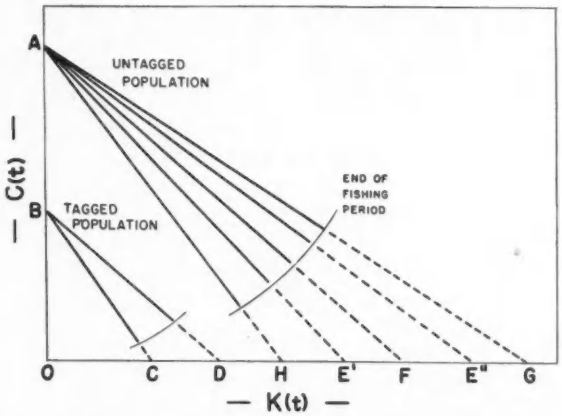

FIGURE 2. The relationship of catch per unit of effort, $C(t)$, to accumulated catch, $K(t)$, under various immigration-emigration ratios. (See text for explanation of symbols.)

If, on the other hand, fish were *immigrating* to the area of fishing at a rate proportional to the stock on hand, then the graph would assume some position AG with a slope less than that of AF. If immigration were not occurring at a rate proportional to the stock on hand but rather say at some constant absolute amount during the period of fishing, then the line AG would be curved (concave upward), tending to become asymptotic with the line $C(t) = R$, where R is the absolute rate of immigration.

In the presence of both immigration and emigration the graph would assume a position AE, somewhere between AH and AG, depending on the ratio of the rates of immigration and emigration. Two possible positions, AE' and AE'' are shown in Figure 2. The problem then arises to determine in what way the slope resulting from the over-all effect of immigration, emigration and fishing mortality differs from that which would have resulted had there been no emigration and immigration. In other words, in what way does the slope of AE differ from AF, or, how does the apparent catchability (k_a) differ from the true catchability (k)? This information may be obtained from a tagging experiment conducted during the same period as that covered in the analysis of the catch-effort data.

As DeLury (1951) points out, the trend in catch per unit of effort of tagged fish is related to the accumulated catch of tagged fish in the same way that catch per unit of effort from the whole population is related to the accumulated catch from the whole population, namely

$$C'(t) = k'N'(o) - k'K'(t), \qquad \text{(III)}$$

where $C'(t)$ is the catch of tags per unit of effort, $K'(t)$ is the accumulated catch of tags, k' is the apparent catchability of tagged fish, and $N'(o)$ is the population of tagged fish when $t = 0$. The value of $N'(o)$ may be equated with the number of tagged fish at large at the beginning of the experiment. Thus there is provided a means of testing the extent of emigration, if initial tagging mortality is negligible; or conversely, the extent of initial tagging mortality if emigration is negligible.

Graphically, line BD in Figure 2 represents the relation of catch of tags per unit of effort to the accumulated catch of tags. If tagged fish are distributed throughout the population and are as vulnerable to capture as untagged fish, then line BD would have the same slope as line AF. The only factor which can alter the slope of line BD would be emigration, since there can be no immigration of tagged fish. Thus, a line such as BC would result if tagged fish were emigrating at some rate proportional to the stock of tagged fish on hand. Line BC would have the same slope as line AH and the apparent catchability (k') would be greater than the true catchability expressed by the slope of line BD.

The true catchability (k) of the population may be calculated from the apparent catchability of the tagged fish (k') and the ratio of the estimated to actual number of tagged fish. From Figure 2 it can be seen that k' differs from k in proportion to the difference between the true initial number of tags (OD) and the estimated number (OC). In other words, since k=OB/OD, and OB/OD = OB/OC $\times$ OC/OD,

$$k = \text{slope of BC} \times \text{OC/OD} = \frac{k'N'(o)}{\text{number tagged}}. \qquad \text{(IV)}$$

The product $k'N'(o)$ is taken from the first right-hand term of the equation of the line BC (equation III), as fitted to the catch-effort data for tagged fish.

In a similar manner the slope of line AE measures an instantaneous rate of decrease, or "catchability", $\hat{k}$, which includes the effects of fishing, emigration and immigration. The equation of this line is

$$C(t) = \hat{k}\hat{N}(o) - \hat{k}K(t). \qquad \text{(V)}$$

The term $\hat{k}\hat{N}(o)$ is OA of Figure 2, and $\hat{k}$ = OA/OE; whereas the true catchability k is OA/OF. The original population $N(o)$ is represented by OF; hence:

$$N(o) = OF = \frac{OA}{OA/OF} = \frac{\hat{k}\hat{N}(o)}{k}. \qquad \text{(VI)}$$

Rates of emigration and immigration can also be computed from these data, and from them the actual numbers of emigrants and immigrants. Since the instantaneous rate k' includes the effects of emigration and fishing, whereas k measures fishing only, the difference is a measure of emigration:

$$\text{instantaneous rate of emigration} = k' - k. \qquad \text{(VII)}$$

Similarly, immigration is measured by the difference between $\hat{k}$ and k', but since immigration *adds to* the population, it must be positive; that is,

$$\text{inst. rate of immigration} = -(\hat{k} - k') = k' - \hat{k}. \qquad \text{(VIII)}$$

All these k-values are in terms of one unit of fishing effort. To change them to terms of a time unit, namely the whole fishing season, they can be multiplied by the total effort expended (E):

$$\text{rate of fishing} = p = Ek, \tag{IX}$$

$$\text{rate of emigration} = g = E(k' - k), \tag{X}$$

$$\text{rate of immigration} = h = E(k' - \hat{k}). \tag{XI}$$

These rates, multiplied by the average stock on hand ($\bar{N}$) during the period under review, give the number of fish involved in the activity in question (cf. Ricker, 1944):

$$p\bar{N} = \text{number of fish caught}, \tag{XII}$$

$$g\bar{N} = \text{number of emigrants}, \tag{XIII}$$

$$h\bar{N} = \text{number of immigrants}. \tag{XIV}$$

From equation XII, $\bar{N}$ can be estimated, then from the two following expressions the number of emigrants and immigrants can be computed.

(2) Tagging Estimate

When a comparison is desired between the two estimates of population as obtained from catch-effort data and from tagging data, a difficulty may be encountered in making comparable the periods for which the estimates apply. For example, tagged fish may be liberated during some short interval x and a population estimate obtained by the Petersen method from the ratio of tagged to untagged fish in the catches immediately thereafter. A comparable estimate from catch-effort data alone may be obtained only if the catch per unit of effort is declining at time x or begins to decline immediately thereafter. If such is not the case then the period during which the tagging estimate is to be made must be delayed until that time (y) when the catch per unit of effort of untagged fish first begins to decline. The longer the time interval between x and y the greater the likelihood of error in the tagging estimate, if there is any possibility that the tagged fish are emigrating (or dying faster than the untagged fish).

In the experiment which is to be described tagging was carried out during two brief intervals, one 22 days and the other 6 days before time y, that is, before the catch per unit of effort began to decline. The tags liberated during the first interval constituted 27 per cent of the total release. Since the recoveries at time y from the first tagging amounted to 25.4 per cent of the total recapture at that time, it seemed reasonable to believe that there had been no substantial emigration of the first group from the fishing area up to time y. Accordingly, recoveries from both periods of tagging have been combined for the computation of population size by the Petersen method.

When a fishery is operating in such a way that fish are being selected according to size it is not always possible to liberate a group of tagged fish whose length frequency distribution coincides precisely with that of untagged fish comprising the commercial catch. A certain percentage of the fish which are tagged will be under the commercial size and hence must be regarded as "ineffective". As an illustration of this point the length-frequency polygons of

tagged and untagged (commercial catch) lemon soles used in this experiment are compared in Figure 3. An approximate correction for the percentage of "ineffective" tags is made by removing from polygon A (tagged fish) the number of "per cent units" enclosed by the ascending limbs of polygons A and B (shaded area). In other words, the curve of selection of polygon A (ascending limb) is made to coincide with the curve of selection of polygon B.

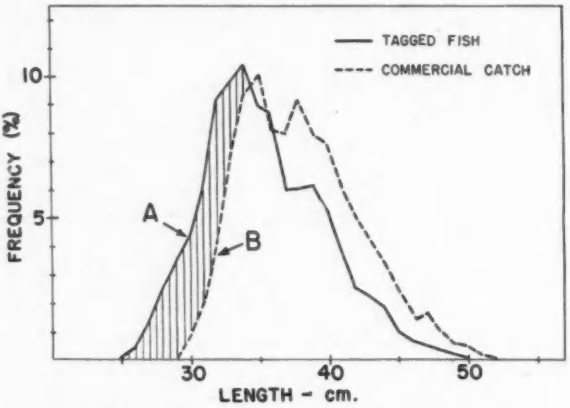

FIGURE 3. Length-frequency polygons of tagged lemon soles and those comprising the commercial catch.

By graphical means it was found that the area enclosed by the ascending limbs of polygons A and B was equal to 23.9 "per cent units". Thus, since 3,003 tagged fish were liberated, only 3,003 $\times$ 0.761 or 2,285 tagged fish could be expected to be of effective size. Since it is assumed that all size-groups of tagged fish are equally vulnerable to recapture, the recoveries of effective tags would be 0.761 of the actual recovery.

RESULTS

(1) Estimates from Tagging Data Alone

Where an open population is involved, estimates by the Petersen method must be made as soon after tagging as possible, since untagged fish may begin to immigrate into the tagging area and hence the estimates of the population will become too high. However, it may be necessary to delay the estimate until the tagged fish have mingled completely with the untagged fish or possibly until they have overcome the effects of tagging and become as vulnerable to capture as the untagged fish. Whether or not a delay is warranted will be indicated by the stability of the estimates made at short (one or two day) intervals after the tagging project has been completed. Table II shows the population estimates for three two-day intervals (1-3) leading up to April 29 (t_o)[1] and for six similar

[1]This date marks the beginning of the period of declining catch per unit of effort.

intervals (4-9) immediately thereafter. It will be noted that relative stability in the estimates is achieved between intervals 5 and 9.

TABLE II. Population estimates from the ratio in the catches of tagged and untagged lemon soles.

Interval	Effective tags recaptured (x)	No. of untagged fish caught (n)	Effective tags at large (X)	Population (millions of fish) ($\hat{N}=nX/x$)
			2255	
1	19	81,000		9.6
			2236	
2	19	46,400		5.5
			2217	
3	27	67,900		5.6
			2190	
4	41	132,100		7.1
			2149	
5	74	173,600		5.0
			2075	
6	45	102,500		4.7
			2030	
7	50	118,800		4.8
			1980	
8	60	146,300		4.8
			1920	
9	47	127,600		5.2

Since it is desired to compute an average estimate of the population for a period as close to t_o as possible, the catches of tagged and untagged fish for intervals 5, 6, and 7 have been combined. Thus, if the number of tag recaptures (x) in these three intervals is 169, the total number of fish caught (n) is 395,069, and the number of tagged fish at large (X) at the beginning of interval 5 is 2,149, then the average population is estimated as:

$$\hat{N} = \frac{nX}{x} = \frac{2{,}149 \times 395{,}069}{169} = 5.02 \text{ million fish.}$$

The 95 per cent confidence limits of sampling error on this estimate, derived from DeLury's equation 1.13 (1951, p. 288), namely,

$$\text{limits of } \hat{N} = \frac{nX}{x \pm 2\sqrt{x\left(1-\frac{x}{n}\right)}},$$

are 4.37 and 5.89 million fish. On the basis of the knowledge that the average weight of individual lemon soles landed during the period of study was 0.937 pounds, the above estimate may be expressed as 4.70 million pounds with corresponding limits of 4.10 and 5.52 million pounds.

(2) Estimates from Catch-Effort Data Alone

Since catch-effort data alone can reveal no information about the size of a population unless the catch per unit of effort is declining, the analysis has been restricted to the period April 29 to June 22. Between April 1 and 28

Table III. Showing daily catch, $c(t)$, effort, $e(t)$, catch per unit of effort, $C(t)$, accumulated effort, $E(t)$, and accumulated catch, $K(t)$, for the period April 29 to June 22, 1950.

Date	$c(t)$	$e(t)$	$C(t)$	$E(t)$	$K(t)$
	lbs. $\times 10^4$	10 *boat-hours*			
April 29	5.045	3.01	1.68	0	0
30	7.423	4.34	1.71	3	7
May 1	9.755	5.25	1.86	7	17
2	6.625	5.43	1.22	12	30
3	4.417	4.33	1.02	17	39
5	5.256	4.71	1.12	21	45
6	4.746	4.01	1.18	26	52
7	6.464	5.96	1.09	30	58
8	6.280	5.60	1.12	36	67
10	7.537	5.83	1.29	42	75
13	6.234	4.84	1.29	48	85
14	5.811	5.80	1.00	53	93
15	5.688	5.69	1.00	59	101
17	5.780	6.16	0.94	64	109
20	3.887	3.24	1.20	70	117
21	4.330	3.61	1.20	73	122
22	4.254	3.60	1.18	77	128
23	4.263	3.54	1.20	81	134
25	4.121	3.44	1.20	85	140
26	2.541	2.45	1.04	88	146
27	4.250	3.62	1.17	90	149
29	4.490	3.77	1.19	94	155
30	5.126	5.43	1.02	98	161
31	4.787	5.11	0.94	103	168
June 1	4.229	4.37	0.97	108	174
2	3.450	3.87	0.89	112	180
3	4.648	4.86	0.96	116	185
4	5.600	5.84	0.98	121	191
5	6.120	6.48	0.94	127	199
6	5.240	5.46	0.96	133	207
7	4.200	3.74	1.12	138	214
8	2.510	3.36	0.78	142	220
9	5.570	5.16	1.08	145	223
16	2.367	2.36	1.00	150	231
17	4.106	4.14	0.98	152	233
18	5.870	5.74	1.02	156	239
19	2.469	3.43	0.72	162	247
20	1.439	1.80	0.80	165	250
21	1.091	1.57	0.70	167	252
22	0.623	1.00	0.62	169	253

there was an increase in catch per unit of effort (see Appendix II) which may be attributed to the progression of the main run into the area where it could be exploited. In Table III the catch per unit of effort, $C(t)$, for each day has been obtained by dividing the total daily catch, $c(t)$, by the total daily effort, $e(t)$. The cumulative effort, $E(t)$, is obtained by adding the daily values of $e(t)$.

The records of catch shown in Table III are those for which the amount of effort is known. In computing the column of values for $K(t)$, i.e. the cumulative catch, consideration has had to be given to 431,000 pounds of fish caught by United States vessels and 215,000 pounds caught by Canadian vessels for which no information on effort was available. This additional 646,000 pounds has been broken down and distributed in proportion to the catch data for which effort was known. Details of the derivation of the $K(t)$ values shown in the table are given in Appendix III.

Values of $C(t)$ and $K(t)$ have been plotted in Figure 4. The straight line fitted to the points by least squares has the equation

$$C(t) = 1.434 - 0.00246K(t),$$

where $C(t)$ is in 10,000 lb. per 10 boat-hours. Converting $C(t)$ to pounds per boat-hour, the equation becomes:

$$C(t) = 1{,}434 - 0.000246K(t).$$

It follows from equation V that 0.000246 may be identified with $\hat{k}$, the apparent catchability; and 1,434 with $\hat{k}\hat{N}(o)$. Hence,

$$\hat{N}(o) = 1434/0.000246 = 5.83 \text{ million pounds.}$$

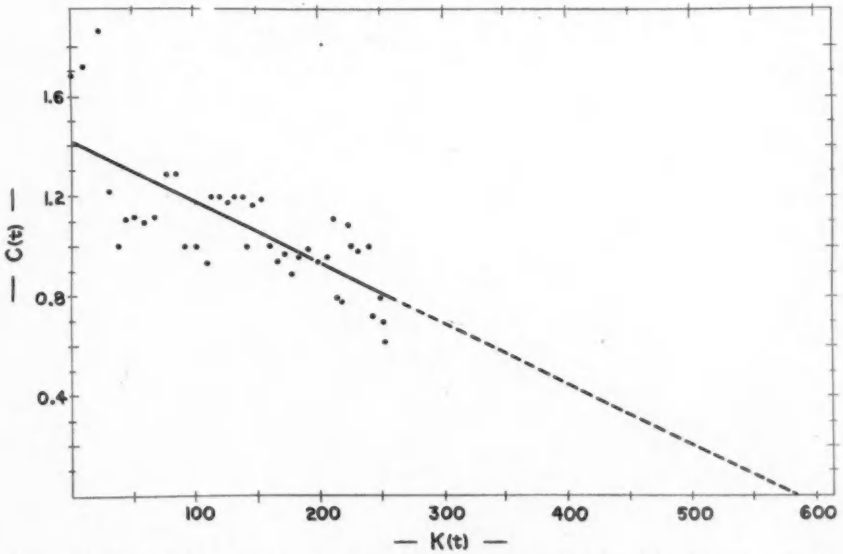

FIGURE 4. The relation of catch per unit of effort to accumulated catch of lemon soles in Hecate Strait from April 29 to June 22, 1950.

This estimate, which can be called the "apparent initial population" may be compared with the estimate of 4.70 million pounds derived from tags alone. $\hat{N}(o)$ could be used as an estimate of population if the population were closed, in the sense of having emigration constantly balanced by immigration and hence $\hat{k} = k$, the true catchability. The fact that the catch-effort estimate is greater than that obtained from tagging suggests that the rate of immigration was *greater* than that of emigration and hence that $\hat{k}$ and k are not equivalent. Of course, this conclusion would be based on the provision that there had been no error in the data which could have caused the tagging estimate to be too high.

It remains then to determine whether the difference may be attributed to imbalance between the amount of emigration and immigration of untagged fish or to an error in the assumptions about the tagging data. This may be accomplished by running a catch-effort analysis on the tagged members of the population.

(3) The Use of Catch-Effort Data in Conjunction with Tagging Data

(*a*) estimation of the tagged population

As pointed out by DeLury (1951), in a sequence of catch-effort records in which the effort expended during the t^{th} interval is $e(t)$ and the total catch is $c(t)$ of which $c'(t)$ are tagged and $c''(t)$ are not tagged, then three estimates

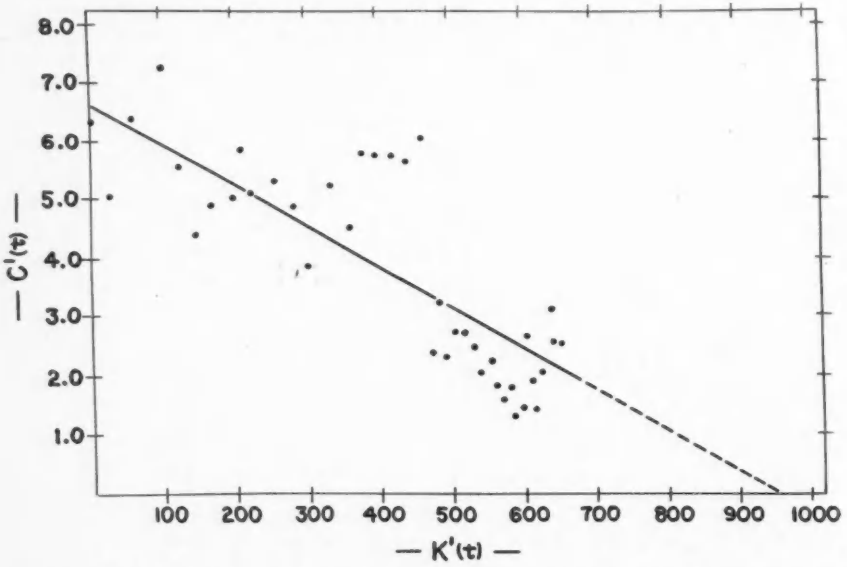

Figure 5. The relation of number of tagged fish caught per unit of effort to accumulated catch of tags in Hecate Strait from April 29 to June 22, 1950.

TABLE IV. Catch and catch per unit of effort of tagged lemon soles. (See text for explanation of symbols.)

Date	$c'(t)$	$e(t)$	$C'(t)$	$K'(t)$
	pieces	10 *boat-hours*		
April 29	19	3.01	6.30	0
30	22	4.34	5.07	19
May 1	34	5.25	6.48	41
2	40	5.43	7.36	75
3	24	4.33	5.54	115
5	21	4.71	4.46	139
6	20	4.01	4.98	160
7	30	5.96	5.03	180
8	29	5.60	5.18	210
10	31	5.83	5.32	239
13	24	4.84	4.96	270
14	23	5.80	3.96	294
15	30	5.69	5.27	317
17	28	6.16	4.54	347
20	19	3.24	5.86	375
21	21	3.61	5.81	394
22	21	3.60	5.81	415
23	20	3.54	5.65	436
25	21	3.44	6.10	456
26	7	2.45	2.45	477
27	12	3.62	3.31	484
29	9	3.77	2.38	496
30	15	5.43	2.74	505
31	14	5.11	2.74	520
June 1	11	4.37	2.51	534
2	8	3.87	2.07	545
3	11	4.86	2.26	553
4	11	5.84	1.88	564
5	11	6.48	1.69	575
6	10	5.46	1.83	586
7	5	3.74	1.33	596
8	5	3.36	1.48	601
9	14	5.16	2.71	606
16	4	2.36	1.69	620
17	6	4.14	1.44	624
18	12	5.74	2.09	630
19	11	3.43	3.20	642
20	5	1.80	2.77	653
21	4	1.57	2.54	658
22	2	1.00	2.00	662

of the catch per unit of effort may be calculated, $C(t) = c(t)/e(t)$, $C'(t) = c'(t)/e(t)$ and $C''(t) = c''(t)/e(t)$. Corresponding accumulated catches of $K(t)$, $K'(t)$ and $K''(t)$ may also be calculated. Since the number of tagged individuals in the daily catches of lemon soles formed only a very small fraction

of the daily catch of untagged fish, the data on $c''(t)$, $C''(t)$ and $K''(t)$ for present purposes are considered to be equivalent to those on $c(t)$, $C(t)$ and $K(t)$.

The catch of tags per unit of effort, $C'(t)$, and accumulated catch of tagged fish, $K'(t)$, have been entered in Table IV. In Figure 5, values of $C'(t)$ have been plotted against values of $K'(t)$ for the period April 29 to June 22. The straight line fitted to these points by least squares has the equation

$$C'(t) = 6.66 - 0.00695K'(t).$$

By converting $C'(t)$ to terms of number of tags retaken per boat-hour, this equation becomes

$$C'(t) = 0.666 - 0.000695K'(t).$$

On comparing this with equation III, it will be seen that $k' = 0.000695$ and $k'N'(o) = 0.666$, whence

$$N'(o) = 958.$$

$N'(o)$ is an estimate of the tagged population when $t = 0$, that is, at the beginning of the experiment. Although 3,003 tagged fish were liberated, only 2,285 were of effective commercial size. Of the latter number 95 had been recaptured prior to April 29 (t_o). Thus a maximum of 2,190 effective tags were at large when the experiment began. The actual population of tagged fish was therefore over two times as great as that calculated from the catch-effort analysis. The difference reflects the influence of those factors tending to remove tagged fish from the population, namely, emigration, tagging mortality and natural mortality.

(*b*) EVALUATION OF THE TRUE CATCHABILITY

The apparent catchability of untagged fish ($\hat{k}$), as obtained from equation V was 0.000246, whereas the apparent catchability of tagged fish (k') as obtained from equation III was 0.000695. The difference is a reflection of the differential effect of immigration and emigration. The former is influenced by both immigration and emigration, while the latter is influenced by only emigration. The lines representing equations III and V may be identified with lines BC and AE, respectively, in Figure 2.

From equation IV, the true catchability (k), which is the slope of line BD, is equal to

$$k = \frac{k'N'(o)}{\text{number tagged}}.$$

In the foregoing section it was found that $k'N'(o) = 0.666$. Since the number of effective tagged fish at large at t_o was 2,190, then it follows that the true catchability (k) equals 0.000304.

(*c*) NEW ESTIMATE OF THE INITIAL POPULATION

An estimate of the true catchability having been obtained, it is now possible to obtain an estimate of the initial population of untagged fish which is

uninfluenced by emigration and immigration. From the equation of the line in Figure 4, it was found that $\hat{k}\hat{N}(o) = 1{,}434$ (page 471). Since $k = 0.000304$, an estimate of $N(o)$ can be derived from equation VI:

$$N(o) = \frac{\hat{k}\hat{N}(o)}{k} = \frac{1{,}434}{0.000304} = 4.72 \text{ million pounds.}$$

This estimate of the initial population is in remarkable agreement with that obtained from tagging data alone (4.70 million pounds). The agreement points up the fact that imbalance between the rates of emigration and immigration accounts for the difference between the tagging estimate and the apparent population estimated from catch-effort data alone (4.70 million as compared with 5.83 million).

(*d*) EVALUATION OF EMIGRATION AND IMMIGRATION

The instantaneous rate of emigration (equation VII) is the difference between the apparent catchability of tagged fish (k') and the true catchability (k), namely,

$$k' - k = 0.000695 - 0.000304 = 0.000391.$$

The instantaneous rate of immigration (equation VIII) is measured by the difference between k' and $\hat{k}$, namely,

$$k' - \hat{k} = 0.000695 - 0.000246 = 0.000449.$$

In order to convert these k values, which are in terms of one unit of fishing effort, to a time scale in terms of the whole period of study, it is necessary to multiply each by the total fishing effort expended during that period. From catch records providing information on effort, it was found that 1.88 million pounds of lemon sole were produced by 1,700 boat-hours of fishing. However, the total catch during the period was 2.54 million pounds. Assuming simple proportionality, it may be estimated that the total expenditure of effort (E) was 2,285 boat-hours.

From equations IX, X and XI, it follows that

rate of fishing $= p = Ek = 2{,}285 \times 0.000304 = 0.695$;

rate of emigration $= g = E(k'-k) = 2{,}285 \times 0.000391 = 0.893$;

rate of immigration $= h = E(k'-k) = 2{,}285 \times 0.000449 = 1.026$.

Estimates of the numbers (or weights) of emigrants and immigrants during the period of study (equations XIII and XIV) are dependent on knowledge of $\bar{N}$, the average stock on hand during the period. This is obtained from equation XII.

$$\bar{N} = \frac{\text{weight of fish caught}}{p} = \frac{2.54}{0.695} = 3.65 \text{ million pounds.}$$

It follows that

$$\text{weight of emigrants} = g\bar{N} = 0.893 \times 3.65 = 3.26 \text{ million pounds;}$$

$$\text{weight of immigrants} = h\bar{N} = 1.026 \times 3.65 = 3.74 \text{ million pounds.}$$

Part of the weight of immigrants would be due to growth in weight of individuals in the original stock, while part of the weight of emigrants would be due to natural mortality in the original stock. However, neither of these factors need be accounted for, since their effects are presumed to be of minor consequence (see page 462).

The developments thus far may be summarized as follows: It has been estimated that, at the beginning of the period under consideration, a population of 4.72 million pounds of lemon sole was present on the Hecate Strait fishing grounds. During the period an estimated 3.26 million pounds of fish moved out of the fishing area and 3.74 million pounds moved in. The catch by the fishing fleet during this period was 2.54 million pounds.

(4) Estimation of the Total Stock

There arises now the problem of determining (*a*) the size of the stock present during the period of the experiment, (*b*) the size of the stock present during the whole of the 1950 fishing season, and (*c*) the size of the entire adult stock in the region of the Hecate Strait Bank.

(*a*) The population present during the period of experiment may be considered to be the sum of the initial population (4.72 million pounds) and the amount of immigration which occurred during that period, that is, 4.72 + 3.74 or 8.46 million pounds.

(*b*) From Table V an estimate of the *minimum* population for the whole of 1950 fishing season can be obtained by assuming (1) that no emigration occurred during period A, those weeks leading up to the period of the experiment, and (2) that no immigration occurred during period C, those weeks following the period of experiment. (Any immigration which might have occurred during period A would be accounted for in the estimate of the population at the beginning of period B and in the catch during period A. Any emigration which might have occurred during period C would have been accounted for in the estimate of the residual stock at the end of period B.) Thus the catch during period A (1.31 million pounds) plus the stock present during period B (8.46 million pounds) would represent the minimum population for the season, namely 9.77 million pounds.

Table V. Components of catch, emigration and immigration during the 1950 fishing season in Hecate Strait, in millions of pounds.

	Period preceding the experiment[a] A	Period of the experiment B	Period following the experiment C
Total catch	1.31	2.54	0.50
Emigrants	?	3.26	?
Immigrants	?	3.74	?

[a]Period A: Feb. 1-Apr. 28; Period B: Apr. 29-June 22; Period C: June 23-Aug. 31.

An estimate of the *maximum* population may be obtained if it is assumed that the weights of immigrating and emigrating fish are at all times proportional to the catch. The emigrants during period A would be $1.31/2.54 \times 3.26$ or 1.68 million pounds, while the immigrants during period C would be $0.50/2.54 \times 3.74$ or 0.74 million pounds. It follows then that the estimate of the maximum stock would be the sum of this emigration and immigration and the estimate of the minimum stock, namely,

$$1.68 + 0.74 + 9.77 \text{ or } 12.19 \text{ million pounds.}$$

It seems likely that the actual stock present approached neither of these extreme estimates of 9.77 and 12.19 million pounds, but actually occupied some position between the two. Evidence from tagging (presented on page 468), suggests that in the last three weeks of period A there was no substantial emigration from the grounds. Therefore, the maximum estimate is probably too high. For the present it will be assumed that the mean value, 11.0 million pounds, represents the stock which was present during the 1950 fishing season.

(*c*) In large bodies of water the vulnerability of fish to capture is not likely to be uniform from area to area. An accurate estimate may be obtained of the vulnerable population at one particular location, but this may bear no similarity to the total population. The lack of well-defined geographical boundaries to the population can also introduce serious difficulties in making the estimation of the total population. In Hecate Strait, the lemon sole fishery takes place along a small part of the bank between the Warrior Rocks and Dixon Entrance. Catches from other regions along the edge and on top of the bank are by comparison negligible. This may be an indication that the stock migrates through, or inhabits only, that area north of the Warrior Rocks, but it may also be an indication of an economic condition. A fisherman will always direct his effort to those regions where the fish are most concentrated, where he is least likely to suffer loss of time through gear damage and where the distance from shelter is a minimum. The recognized lemon sole grounds in Hecate Strait lie between 30 and 50 fathoms and cover an area of 90 to 100 square miles, whereas the possible ecological habitat of the species along the entire bank (20-50 fathoms) embraces an area of approximately 1,000 square miles. Thus it is conceivable that a substantial body of fish could remain unexploited throughout the fishing season and that the estimates made above would not apply necessarily to the total Hecate Strait population, despite the fact that they involved the entire fishing area and the entire fishing season.

However, evidence contained in data on catch and age composition suggests that the estimates really do apply to substantially the whole population. Over the eight-year period from 1944 to 1951 the Canadian catch from Hecate Strait has averaged approximately 1.2 million pounds per year (Table I), while the United States catch from this area (known only for the years 1948 to 1951) has averaged 0.8 million pounds per year. Assuming that the United States fishery developed in the same manner as the Canadian fishery, the latter figure might be reduced to 0.6 million pounds as an average for the eight-year period. Therefore an estimate of the total average annual catch by both countries would be 1.8 million pounds.

The lemon sole age-composition data (Ketchen *et al.*, 1951) show no clearly defined trend in mortality rate, although some evidence of the effects of fishing may be indicated in the data for the extremities of this eight-year period. In Table VI the percentage contributions of age-groups VII, VIII and IX are shown for two periods, 1944-45 and 1950-51. From the averages for each period a weighted mean survival rate has been computed:

Survival rate 1944-45

$$s = \frac{y_8 + y_9}{y_7 + y_8} = \frac{13.3 + 10.1}{17.1 + 13.3} = 0.770$$

Survival rate 1950-51

$$s = \frac{y_8 + y_9}{y_7 + y_8} = \frac{11.7 + 6.6}{18.1 + 11.7} = 0.614$$

TABLE VI. Percentage composition in the catches of age-groups VII, VIII and IX, averaged for the two periods 1944-45 and 1950-51.

Age	1944	1945	Average	1950	1951	Average
VII	14.6	19.6	17.1	18.4	17.8	18.1
VIII	12.1	14.5	13.3	11.9	11.4	11.7
IX	7.9	12.3	10.1	6.8	6.5	6.6

It should be mentioned that data for age-groups younger than VII have been excluded because of incomplete recruitment prior to that age. Because of the way in which the fishery operated in the initial years it is believed that the age-groups older than IX were less available for exploitation than the younger age-groups; hence they too have been excluded from the calculations. In any event, they would not yet reflect, in 1950-51, the full effect of the fishery upon mortality rates in the population.

Since the population prior to 1943 was essentially in a virgin state, the survival rate of 0.770 as obtained from the 1944-45 data is considered to be reasonably close to the *natural* survival rate. Assuming that the 0.156 difference in the rates between the two periods is the result of mortality due to fishing, it is possible to determine the rate of exploitation and to estimate the total population of adult fish. However, in computing the rate of exploitation three possibilities must be considered regarding the manner in which natural mortality operates.

(1) If all the natural mortality occurs prior to the fishing season, then the seasonal mortality rate from fishing (m) will be some fraction of the survivors after natural mortality, namely $m(1 - 0.23)$ or $0.77\ m$. The survival rate after fishing has taken its toll will be $0.77 - 0.77\ m$, which, when equated to the known final survival rate of 0.614, yields m=0.202, the fishing mortality rate. Thus the rate of exploitation (μ) is 0.77×0.202 or 0.156.

Knowing the average annual catch to be about 1.8 million pounds, an estimate of the total average population of adult fish turns out to be 1.8/0.156 or 11.5 million pounds.

(2) If the fishing mortality occurs before any natural mortality has taken place, then the survivors after fishing will be $1 - m$, where m is the seasonal rate of fishing mortality. The ensuing natural mortality will be $0.23(1 - m)$ and the final survival rate will be $(1 - m) - 0.23(1 - m)$ which, as above, will be equal to 0.614. This yields $m = 0.202$, which in this case will be equivalent to μ, the rate of exploitation.

Using this rate of exploitation, the population estimate becomes 1.8/0.202 or 8.9 million pounds.

(3) A slightly more complicated situation arises when natural and fishing mortality operate concurrently. From the total seasonal mortality rate, a, which is $1 - 0.614$ or 0.386, the total instantaneous mortality rate (i) is found to be 0.488. From the total seasonal rate of natural mortality (n), which is 0.230, the instantaneous rate (q) is found to be 0.261. The instantaneous rate of fishing, p, is $0.488 - 0.261$, or 0.227, by definition (Ricker, 1944, p. 26). Hence the fraction of fish removed by fishing will be:

$$\mu = 0.386 \times 0.227/0.488 = 0.180$$

Using this rate of exploitation the population estimate becomes 1.8/0.180 or 10.0 million pounds.

Since the survival rates cannot be very accurately estimated, it does not matter greatly which of these three estimates is the best. The first agrees very closely with that of the mean population present in 1950, as derived on page 477. All three are of the same order of magnitude as the earlier estimate, and hence suggest that no large segment of the population in 1950 was inaccessible to capture, regardless of the restricted locality and season of fishing.

DISCUSSION

With the aid of information on tag recoveries and on trends in catch per unit of effort, three estimates have been obtained of the Hecate Strait lemon sole population as it existed on the fishing grounds at the end of April 1950. These estimates are as follows:

4.70 million pounds (Petersen estimate);
5.83 million pounds (DeLury estimate);
4.72 million pounds (modified DeLury estimate).

The Petersen estimate was derived from tagging information only and was based on the assumption that no untagged fish had immigrated into the fishing area before the estimate was made. The DeLury estimate was derived from catch-effort information only and was based on the hypothesis that the population was closed, in the sense that emigration was constantly balanced by immigration. The fact that the estimate was considerably greater than that obtained from tagging suggested that the above assumption was not justified and that the amount of immigration must have considerably exceeded the amount of emigration throughout the period of the experiment.

An extension of the DeLury method, employing information on the trend in the catch/effort of tagged fish showed that this was true. The weight of fish which immigrated was 15 per cent greater than that of fish which emigrated (3.74 million pounds as compared with 3.26).

Taking into account this difference a new estimate of 4.72 million pounds was obtained for the population at the beginning of the period of study. The remarkable agreement between this estimate and that obtained from tagging tends to dispel some of the common fears about the efficacy of the tagging method. For example, had there been an appreciable initial tagging mortality or a marked difference in the catchability of tagged and untagged fish, no such agreement would have been achieved.

The extension of the DeLury method to account for emigration and immigration has greatly increased its applicability to the dynamic and complicated situations presented by populations inhabiting large bodies of water. There is no direct evidence to support (or deny) the assumption, used in this extension, that immigration occurs at a rate proportional to the stock on hand. But since the immigration is a post-spawning migratory movement, one might reasonably expect the number of fish entering to taper off; and the assumption of a constant instantaneous rate used above does of course demand that the number entering should decrease as the stock itself decreases.

The error caused by making the above assumption would not be great, even if the daily number of immigrants were actually constant over the whole of the experimental period while emigration and fishing remained as before: The latter are characterized by instantaneous rates g and p, respectively, or i in all; and (in this example) i was determined, from the data on tagged fish only, as being 1.588, a figure which is independent of the way in which immigration may have occurred. It can be shown (cf. Ricker, 1944, p. 31) that the losses from a group of I immigrants arriving in uniform absolute numbers in successive days are $I(i - a)/i$, and their survivors are $I \cdot a/i$, where a is the seasonal rate of loss corresponding to the instantaneous rate i, or 0.796 in this case. Survivors of those fish present at the beginning of the experiment are of course $N(o).(1 - a)$. The total survivors are the sum of these two, and this sum will bear to the original $N(o)$ the same ratio as the initial to the final catch per unit of effort in Figure 4, which is 1.434 to 0.812, approximately. Thus it follows that

$$\frac{N(o)}{N(o).\,(1-a) + I \cdot a/i} = \frac{N(o)}{0.204\ N(o) + 0.501\ I} = \frac{1.434}{0.812}.$$

Hence $I = 0.724\,N(o)$, a result not greatly different from $I = 0.792\,N(o)$ obtained by the hypothesis used earlier. The hypothesis of uniform absolute recruitment or immigration would of course imply that the line to be fitted to Figure 4 should be somewhat concave upward, but not enough to make the ratio of initial to final $C(t)$ significantly different from the 1.434/0.812 used above.

Other schemes of introducing the immigrants can be explored, but nothing within reason makes the estimate of their relative numbers seriously different from the one originally computed. The criterion of reasonableness is, of course,

any hypothesis which will not disagree seriously with the course of the decline in catch per unit of effort indicated by the points (not necessarily the *line*) in Figure 4.

Questions of economic importance depend on the interpretation of the estimates of the *accessible* and *total* adult populations in Hecate Strait. The population exploited in the 1950 season was calculated from catch-effort and tagging data and was found to lie somewhere between 9.8 and 12.2 million pounds. Because the extremes were believed to represent unlikely situations, a mean value of 11.0 million pounds was adopted. Estimates of the average total stock in the strait were derived from information on the average annual catch and the average rate of exploitation. These estimates ranged from 8.9 to 11.5 million pounds, depending on how natural mortality operates; and are of the same order of magnitude as the estimate of the population fished. This suggests that despite the size of the Hecate Strait area and the limited region of fishing within that area, a very large segment of the population was accessible to the fishery in the 1950 season. If this is true, then important considerations arise regarding the catches of recent years. Total catches for the years 1948-51 (Table I) were approximately 1.9, 1.7, 4.4 and 2.0 million pounds, respectively. Assuming a constant population level of say 9.0 million pounds, these catches would represent 21, 19, 49 and 22 per cent, respectively, of the total stock. At a population level of say 11.0 million pounds the same catches would represent 17, 15, 40 and 18 per cent, respectively, of the total stock. The assumption of a constant population level would appear untenable, however, insofar as the 1951 fishery was concerned. There is no evidence in the age composition that the heavy removal of 40-50 per cent experienced in the 1950 season was compensated for by heavy recruitment of young fish in the following season. Hence, while the low availabilities (catch per unit of effort) in the 1948 and 1949 seasons probably were the result of low catchability (due either to unfavorable fishing conditions or to the absence of part of the stock from the fishing grounds), the low availability in the 1951 season was probably the result, at least in part, of decreased abundance.

It cannot be emphasized too strongly, however, that the reliability of this interpretation depends heavily upon the accuracy of the survival rates used in computing the total stock. The results as they stand suggest that the Hecate Strait stock of lemon soles, although only lightly exploited in the majority of years since the origin of the fishery, was heavily exploited in 1950 as a result of an unusual combination of high catchability and heavy fishing effort. Under such conditions, it is likely that the maximum production consistent with sustained yield is being approached.

SUMMARY

(1) Estimates of a population of lemon sole (*Parophrys vetulus*) inhabiting Hecate Strait, British Columbia have been computed for the 1950 fishing season with the aid of tagging and catch-effort information.

(2) A Petersen-type estimate from tag returns for the beginning of May was 4.70 million pounds (95 per cent limits — 4.37 and 5.89 million pounds) of adult fish.

(3) Computation based on the relation of catch per unit of effort to accumulated catch throughout the months of May and June have yielded an estimate of 5.83 million pounds for the initial adult population.

(4) By means of information obtained from the catch of tags per unit of effort during the two-month period it has been possible to demonstrate that the difference between the two estimates was due to imbalance between emigration and immigration. This imbalance, being expressed quantatively, has been used to re-estimate the initial population. This was found to be 4.72 million pounds, or approximately the same as that obtained from tagging.

(5) On the basis of information on the relation of emigration to immigration and on the catch during the period of the experiment, an estimate with probable limits of 9.8 and 12.2 million pounds was obtained for the "accessible" adult population—that which was present on the fishing grounds during one part or another of the season of the fishery in 1950.

(6) Information on the average catch over the period 1944-51 and the average survival rate as obtained from age composition has been used to determine the *total* adult population for Hecate Strait. Depending on the pattern of natural mortality, the estimates ranged from 8.9 to 11.5 million pounds.

(7) That the estimates of *accessible* and *total* adult populations are of the same order of magnitude suggests that in 1950 (a year of exceptionally high production) the whole stock or a very large segment of it, became accessible to the fishing fleet. A removal of over 40 per cent of the stock may have occurred in that season and may have been responsible to some extent for the lowered availability of fish in the following season of 1951.

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APPENDIX I. Lemon sole tag recaptures during the 1950 fishing season.

Period of recapture	Date of tagging		Total recaptures	Percentage from first tagging
	April 7	April 23		
April				
I	—	—	—	—
II	5	—	5	100
III	28	—	28	100
IV	32	70	102	31
May				
I	62	190	252	25
II	27	99	126	21
III	44	119	163	20
IV	51	143	194	26
June				
I	25	62	87	29
II	8	21	29	27
III	18	53	71	25
IV	3	7	10	30
July				
I	7	23	30	23
II	10	22	32	31
III	7	22	29	24
IV	8	10	18	44
August				
I	3	7	10	30
II	1	5	6	17
III	—	—	—	—
IV	—	—	—	—
September				
I	4	3	7	50
II	—	2	2	0
III	2	5	7	28
IV	—	—	—	—
October				
I	—	—	—	—
II	1	1	2	50
III	—	—	—	—
IV	—	—	—	—
Unassigned	14	34	48	
Total recaptures	360	898	1258	28.6
Total tagged	823	2180	3003	27.4

APPENDIX II. Daily catch, $c(t)$, effort, $e(t)$, catch per unit of effort, $C(t)$, accumulated effort, $E(t)$, and accumulated catch, $K(t)$, for the period April 1 to June 22, 1950.

Date	$c(t)$[a]	$e(t)$[b]	$C(t)$	$E(t)$	$K(t)$	Date	$c(t)$[a]	$e(t)$[b]	$C(t)$	$E(t)$	$K(t)$
April 1	3.779	6.01	0.63	0	0	May 14	5.811	5.80	1.00	123	131
2	4.749	7.11	0.67	6	4	15	5.688	5.69	1.00	129	137
3	4.047	6.75	0.60	13	9	17	5.780	6.16	0.94	135	143
5	2.290	2.80	0.82	20	13	20	3.887	3.24	1.20	141	149
6	1.756	2.10	0.84	23	15	21	4.330	3.61	1.20	144	153
7	3.613	4.60	0.79	25	17	22	4.254	3.60	1.18	148	157
9	4.536	5.60	0.81	30	21	23	4.263	3.54	1.20	152	161
15	3.204	4.26	0.75	36	26	25	4.121	3.44	1.20	156	165
16	4.336	5.28	0.82	40	29	26	2.541	2.45	1.04	159	169
17	1.381	1.68	0.82	45	33	27	4.250	3.62	1.17	161	172
18	3.935	4.33	0.91	47	34	29	4.494	3.77	1.19	165	176
20	2.587	2.57	1.01	51	38	30	5.126	5.43	1.02	169	181
21	2.311	1.80	1.28	54	41	31	4.787	5.11	0.94	174	186
22	3.733	2.92	1.38	56	43	June 1	4.229	4.37	0.97	179	191
23	3.924	3.28	1.20	59	47	2	3.450	3.87	0.89	183	195
24	2.238	2.03	1.10	62	51	3	4.648	4.86	0.96	187	198
25	2.145	1.96	1.10	64	53	4	5.600	5.84	0.98	192	203
26	3.671	4.03	0.90	66	55	5	6.120	6.48	0.94	198	209
28	2.735	2.31	1.18	70	59	6	5.240	5.46	0.96	204	215
29	5.045	3.01	1.68	72	62	7	4.200	3.74	1.12	209	220
30	7.423	4.34	1.71	75	67	8	2.510	3.36	0.78	213	224
May 1	9.755	5.25	1.86	79	74	9	5.570	5.16	1.08	216	227
2	6.625	5.43	1.22	84	84	16	2.367	2.36	1.00	221	233
3	4.417	4.33	1.02	89	91	17	4.106	4.14	0.98	223	235
5	5.256	4.71	1.12	93	95	18	5.870	5.74	1.02	227	239
6	4.746	4.01	1.18	98	100	19	2.469	3.43	0.72	233	245
7	6.464	5.96	1.09	102	105	20	1.439	1.80	0.80	236	247
8	6.280	5.60	1.12	106	111	21	1.091	1.57	0.70	238	248
10	7.537	5.83	1.29	112	117	22	0.623	1.00	0.62	240	249
13	6.234	4.84	1.29	118	125						

[a] $c(t)$ in 10,000 pound units.
[b] $e(t)$ in 10 boat-hour units.

APPENDIX III. Derivation of the column of K(t) values shown in Table III (figures in ten thousands of pounds).

Date	$c(t)$ Canadian (effort known)	$c(t)$ Canadian (effort unknown)	$c(t)$ U.S. (effort unknown)	Total $c(t)$	K(t)
April 29	5.04	0.55	1.12	6.71	0
30	7.42	0.84	1.68	9.94	7
May 1	9.76	1.11	2.23	13.10	17
2	6.63	0.75	1.50	8.88	30
3	4.42	0.50	0.99	6.01	39
5	5.26	0.60	1.20	7.06	45
6	4.75	0.53	1.07	6.35	52
7	6.46	0.73	1.46	8.65	58
8	6.28	0.71	1.42	8.41	67
10	7.54	0.86	1.72	10.12	75
13	6.23	0.71	1.42	8.36	85
14	5.81	0.66	1.33	7.80	93
15	5.69	0.64	1.29	7.62	101
17	5.78	0.66	1.33	7.77	109
20	3.89	0.45	0.90	5.24	117
21	4.33	0.50	0.99	5.82	122
22	4.25	0.49	0.99	5.73	128
23	4.26	0.50	0.99	5.75	134
25	4.12	0.47	0.95	5.54	140
26	2.54	0.28	0.56	3.38	146
27	4.25	0.49	0.99	5.73	149
29	4.49	0.51	1.03	6.03	155
30	5.13	0.58	1.16	6.87	161
31	4.79	0.56	1.12	6.47	168
June 1	4.23	0.49	0.99	5.71	174
2	3.45	0.38	0.77	4.60	180
3	4.65	0.53	1.07	6.25	185
4	5.60	0.64	1.29	7.53	191
5	6.12	0.71	1.42	8.25	199
6	5.24	0.60	1.20	7.04	207
7	4.20	0.47	0.95	5.62	214
8	2.51	0.28	0.56	3.35	220
9	5.57	0.64	1.29	7.50	223
16	2.37	0.28	0.56	3.21	231
17	4.11	0.47	0.95	5.53	233
18	5.87	0.66	1.33	7.86	239
19	2.47	0.28	0.56	3.31	247
20	1.44	0.17	0.34	1.95	250
21	1.09	0.13	0.26	1.48	252
22	0.62	0.06	0.13	0.83	253
Totals	188.66	21.47	43.11	253.36	

The Bottom Fauna of Great Slave Lake

By D. S. Rawson
University of Saskatchewan, Saskatoon

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ABSTRACT

The macroscopic bottom organisms of Great Slave Lake were sampled with more than 600 dredgings in the summers of 1944 to 1947. Additional ecological information was obtained from qualitative collections and from the examination of stomach contents of fish. The large area (10,500 sq. mi.) and extreme depth (2,000 ft.) of the lake necessitated special equipment and sampling procedures which are described.

The bottom fauna of Great Slave Lake is typical oligotrophic, dominated by the amphipod *Pontoporeia affinis* and including several species of sphaeriids (*Pisidium*), oligochaete worms and chironomid larvae (mostly *Spaniotoma*). In these respects the bottom population resembles those of Lakes Athabaska, Reindeer, Winnipeg and Michigan. In the extreme depths, 200-600 metres, of Great Slave Lake the bottom fauna is made up of single species of amphipod, ostracod, nematode, oligochaete, sphaeriid and chironomid. Attention is drawn to the contrast between this restricted fauna of a recent glacial lake and the great numbers of species found in ancient lakes such as Baikal and Tanganyika.

The average bottom population for the whole lake is 1,603 organisms per square metre and 3.7 kg. dry weight per hectare. However, in Yellowknife Bay the population is double this general average, while in McLeod Bay, of the east arm, it drops to one-quarter. Edaphic, climatic and morphometric factors are discussed in explaining these differences between areas. The bottom population of the upper 50 metres is fairly heavy. It declines rather rapidly from 50 to 150 metres, but is relatively constant from 200 to 600 metres.

The heavily silted area off the Slave River Delta has a bottom population heavier than that at similar depths elsewhere in the main lake. Oligochaetes and nematodes are more numerous in the silted area while molluscs and ostracods are much reduced. Bottom organisms provide about 40 per cent of the food of the main fish in the lake. Two species of whitefish and two species of suckers obtain more than 90 per cent of their food from bottom organisms.

The average weight of bottom organisms in ten large lakes has been compared and found to show an inverse relation to mean depth. A formula has been derived and a curve drawn to describe this relationship. The implication is that productivity is dominated by morphometric conditions in these large, deep lakes.

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INTRODUCTION

THIS STUDY of the bottom fauna of Great Slave Lake was a part of the investigation of its limnology and fisheries, begun in 1944. The primary aim of this investigation was to examine all the evidence which might be useful in estimating the fish-producing capacity of the lake before it was opened to commercial exploitation. This was done and the results were reported by the writer in two papers (Rawson, 1947a, 1949). More detailed reports on physical limnology (Rawson, 1950) and fish (Rawson, 1951a) have since been published. The present paper is the full report on the bottom fauna studies carried on in the years 1944 to 1947.

Our objective was to sample the bottom macrofauna at all depths and in all areas of the lake. This was necessary in order to estimate the supply of food for bottom-feeding fish and to compare this with that of lakes of known fish-producing capacity. The dredging was as extensive as possible in the time which could be allotted to this phase of the work. A total of more than 600 dredgings may be thought of as extensive sampling, but they are thinly scattered in a lake area of 10,000 square miles. Fortunately, large areas of the open and deeper water regions support comparatively uniform bottom populations.

The qualitative study of the bottom fauna was subordinated in order to leave more time for quantitative sampling. Thus the inshore areas, which are rich in variety of species, were given little attention, and the dominant species of the open water were collected and studied in relation to their place in the food cycle. Nevertheless, the importance for distributional studies of data from a remote area has been recognized, and every effort has been made to place the collections in the hands of specialists for specific determination.

METHODS

THE PLAN OF SAMPLING

The selection of locations for dredging raised the question of how to make best use of a few hundred dredgings to obtain a quantitative picture of the bottom fauna of the whole lake. In a small lake a truly random method of sampling may be feasible. To cover this very large area it was necessary to take advantage of the relative uniformity of distribution in certain depths and areas. Within these restricted areas the distribution of dredgings was essentially at random. In selecting locations for dredging several principles were kept in mind. All the major water areas were criss-crossed with series of dredgings close enough to leave no major gaps. Since the bottom population of the shallow water is more variable than that in the greater depths, the inshore dredgings were taken at close intervals, often a few hundred yards, while those in the offshore area were frequently one to four miles apart. Numerous short series were taken in areas of particular interest such as the Slave Delta and

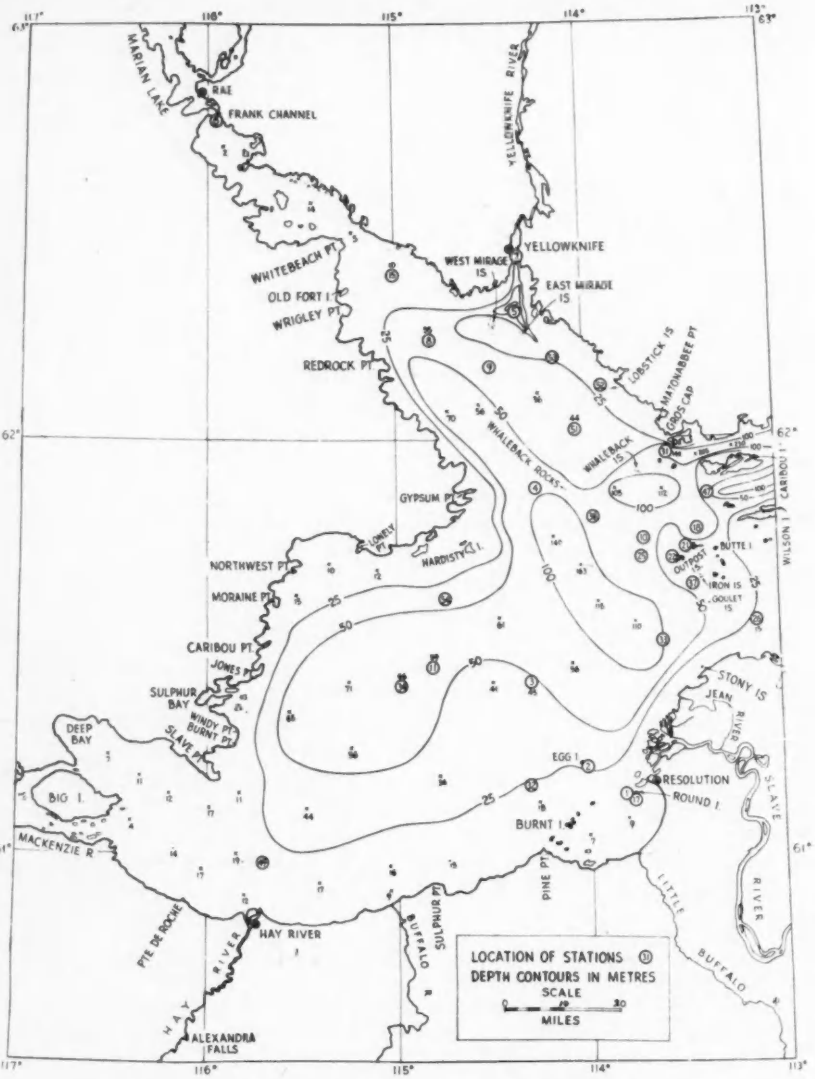

FIGURE 1. Map of the main part of Great Slave Lake showing depth contours.

the 600-metre area in Christie Bay. The number of dredgings in any region was related in a general way to the fraction of the total lake area represented by that region. However, this was not regarded as of primary importance, since averages calculated for the whole lake were arrived at by first calculating the averages for particular regions and then weighting the total according to the relative areas of these regions. The distribution of dredgings in the various parts of the lake may be tabulated as follows:

Main lake (open portion)	115
Resolution and the shallow area to the west	71
North Arm	44
Yellowknife Bay	49
Outpost Islands and Gros Cap	65
The Islands section, including Hearne and Hornby Channels	68
Christie and adjacent bays	143
McLeod Bay	30

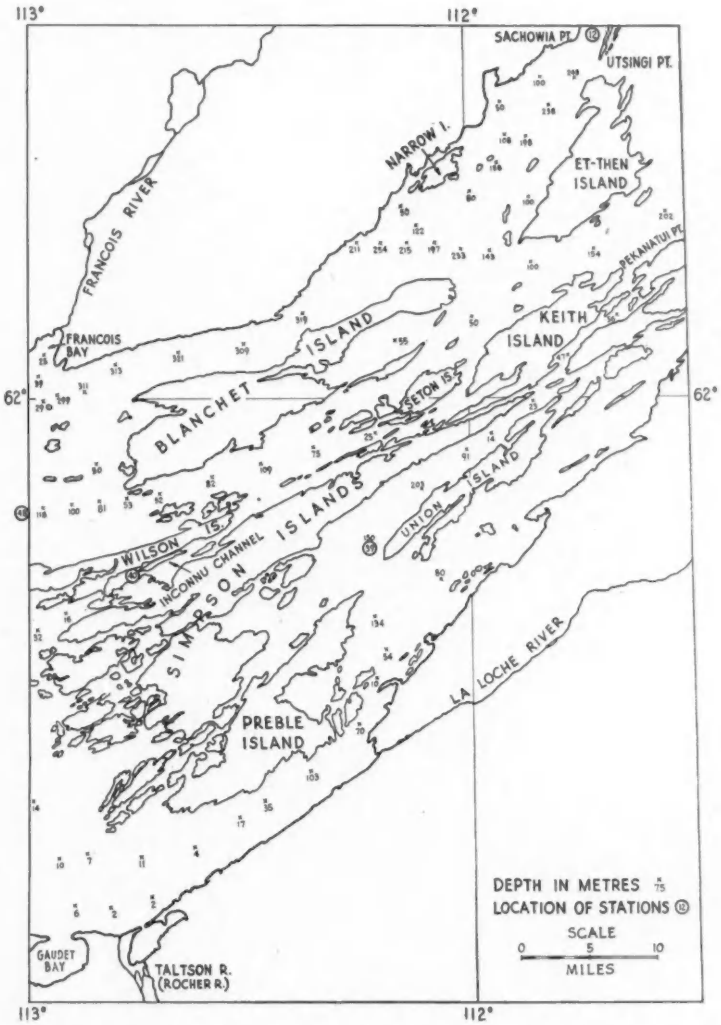

FIGURE 2. Map of the "Islands Section" of Great Slave Lake showing depths.

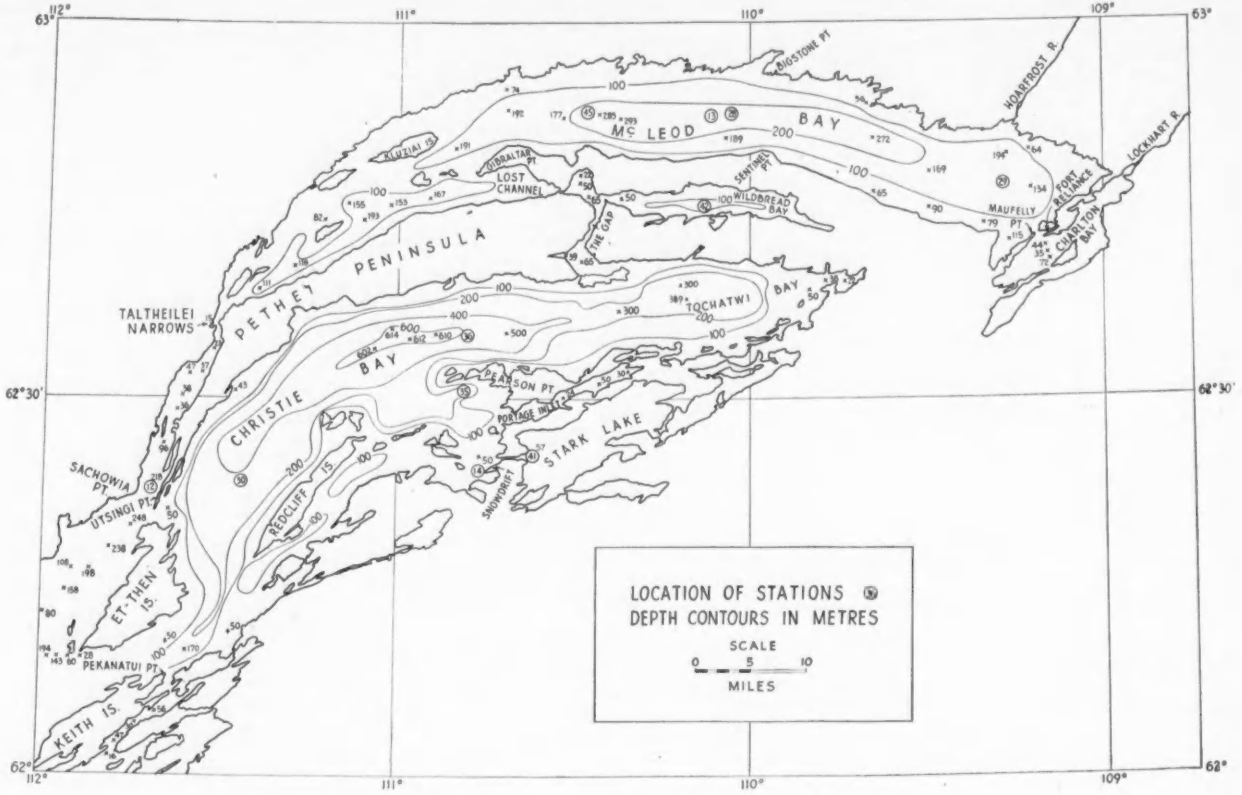

FIGURE 3. Map of the east arm of Great Slave Lake showing depth contours.

These regions may be observed on the maps, Figures 1, 2 and 3, which indicate the various localities referred to in this paper.

The dredging series commonly included 5 to 10 dredgings and were usually taken in a straight line from a point fixed by sighting on convenient landmarks. The position of the dredgings along this line was determined by observing elapsed time at controlled boat speeds. Whenever possible, both ends of a series were "tied in" to known landmarks, and thus small errors, due to drifting or erratic boat speeds, could often be corrected. In the open-water areas courses were held with a 9-inch ship's compass and checked again with available landmarks. The success of these crude methods of survey was attested by the close agreement between our soundings and detailed soundings taken later in the western part of the lake by Hydrographic Survey. Plotting the Great Slave dredgings is not possible on maps small enough for convenient inclusion in this paper. Details of the location of individual dredgings and a complete tabulation of the organisms found in each are on file with the Fisheries Research Board of Canada, Ottawa, and in the Limnology Laboratory of the University of Saskatchewan, Saskatoon.

Dredging Equipment and Procedures

Most of the dredgings were taken with an Ekman dredge of the size commonly referred to as 9-inch; actually, it has an inside area of one-twentieth of a square metre. This dredge worked well on soft bottoms and at moderate depths, but was found to be inefficient at depths beyond 200 metres. It was therefore modified by the addition of two features, Figure 4. A heavy iron flange was attached in such a way that it brought the dredge to an upright position even though it struck the bottom obliquely. Also, a pair of treadles was attached to this flange and coupled with the tripping mechanism so that the dredge closed automatically as soon as both sides of the flange touched the bottom. The modified dredge worked very well, so it was described (Rawson, 1947b) along with a windlass and cable suitable for work in deep water.

A Petersen dredge, Figure 4, was used for sampling hard bottom which occurred chiefly in shallow water. Clay and fine gravel were sampled effectively with this apparatus, but occasional areas of large stones or bare rock were not sampled quantitatively. Drag dredges were used occasionally for qualitative sampling over various types of bottom. The Beauchamp trawl, Figure 4, was found most useful in the special study of *Mysis* and *Pontoporeia* which has been reported by Larkin (1948). A galvanized dredge bucket suitable for use with both Ekman and Petersen dredges was constructed, Figure 4. It was a heavy-gauge galvanized iron, of sufficient volume to hold a dredging with little danger of loss by splashing, and flared enough to allow convenient nesting for storage. The width was such that the jaws of the Ekman entered easily, but the side pivots of the latter supported its weight while the sample was emptied by opening the jaws.

Washing and Analysis of Bottom Organisms

Two kinds of washing equipment were used to recover the organisms from dredgings. A set of three screens on nesting wooden frames 18 inches (45.7 cm.) square was similar to those described by the author, (Rawson, 1930). The upper screen was of wire, 25 meshes per sq. cm. and the others of bolting cloth of 50 and 225 meshes per sq. cm. The other apparatus was a dredge-washing pail illustrated in Figure 4. It has a narrow mouth, 25 cm. in diameter, and a wide bottom, 35 cm. in diameter, and covered with bronze wire screen 250 meshes per sq. cm. The dredging was placed in the pail which was then held over the stern of the boat and rotated by means of the handle. Three obliquely placed fins extending out about 2.5 cm. from the inside of the pail served to increase turbulence and hasten straining. When all the mud had been washed through the screen the pail was inverted over another screen 250 meshes per sq. cm. and the organisms and debris washed down to the flat screen where they could be easily sorted.

The triple screens were effective with all types of bottom material and were advantageous if much debris was retained by the screens. However, the screen-bottomed pail

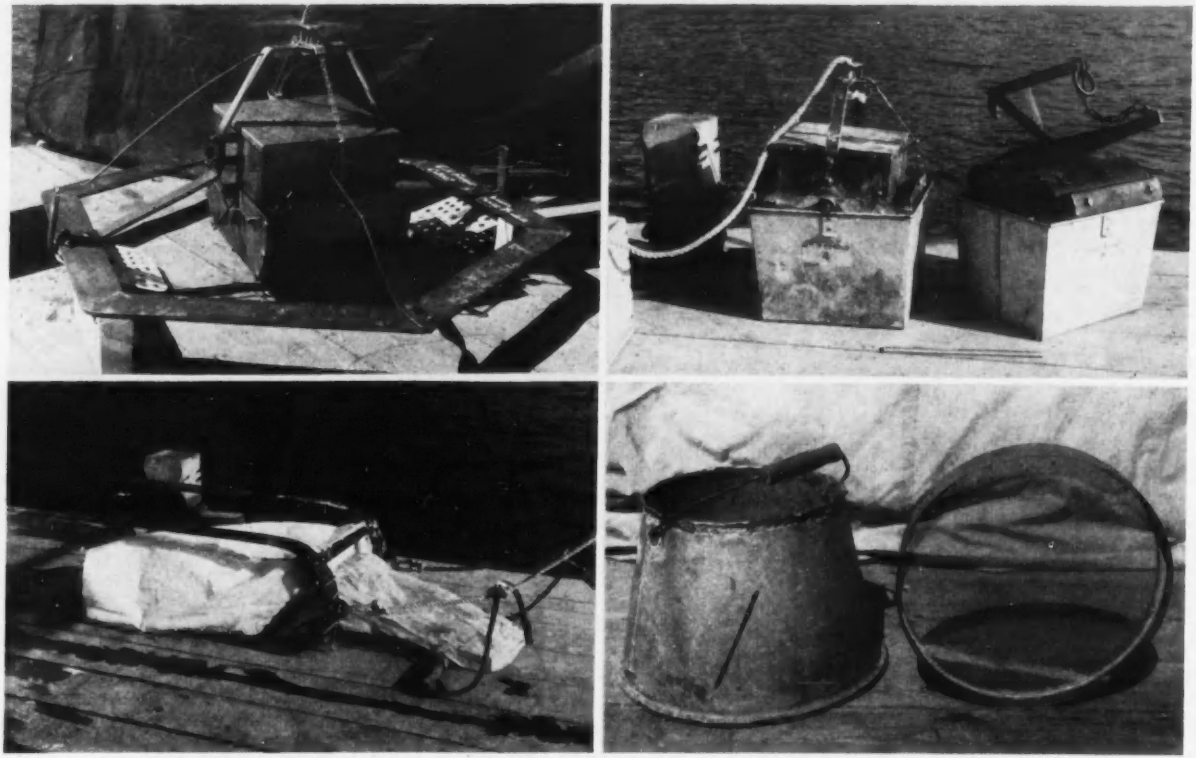

FIGURE 4. Equipment used in dredging. *Above*, automatic-closing modification of the Ekman dredge and buckets to accommodate dredgings with Ekman and Petersen dredges. *Below*, the Beauchamp trawl and the dredge-washing pail.

was considerably easier and faster, if the bottom was mostly of fine particles as it is in much of the open-water area of Great Slave Lake. The use of the pail avoided the necessity of lifting many pails of water and there was a much smaller area of screen to be examined for organisms. Credit for the introduction and improvement of this technique should go to Dr. J. G. Oughton who was a member of the field party in 1944-1946.

The organisms were removed at once from the residue, thus taking advantage of movements as an aid in locating them. Preservation was in vials of 80 per cent alcohol in most cases or sometimes in formalin if there were no molluscs present. The samples were taken to the laboratory for final enumeration, identification and weighing with a quick-registering torsion balance sensitive to 1 milligram. Care was used in making wet-weight determinations that the organisms had no excess fluid among them, nor were they allowed to dry, i.e. to lose internal fluids which would reduce their weight below their live weight. The molluscs in each dredging were weighed separately, and the appropriate percentage was deducted for shell weight before calculating the weight of the dredging. Several large composite samples were dried to determine that dry weight of the dominant organisms in the bottom fauna of Great Slave Lake averaged 15 per cent of the wet weight.

SPECIES COMPOSITION OF THE BOTTOM FAUNA

The organisms recovered from the dredgings and a few collected along shore have been forwarded to the appropriate specialists for specific determination. The following lists indicate the species reported.

Porifera

The freshwater sponges have been identified by Dr. M. C. Old, Hofstra College, New York, who reports two species.

Spongilla fragilis Leidy. Yellowknife Bay and Gros Cap areas at depths of 3 to 7 metres.

Spongilla, probably *lacustris* (L.). Shallow water, Yellowknife Bay.

Coelenterata

Hydra sp. A few specimens of hydra were collected in the shallow water of Yellowknife Bay.

Bryozoa

The bryozoans were identified by Dr. Makoto Toriumi of Tohoku University, Japan. Our collections included four species.

Paludicella articulata (Ehr.). Collected from Yellowknife Bay at 20 metres and Jones Bay at 12 metres.

Fredericella sultana (Blum.). Nine collections ranging from Jones Bay on the west shore to Yellowknife and east to Reliance on McLeod Bay. Specimens were brought up by dredging from depths of 1.5 to 33 metres.

Plumatella repens, var.*typica* (L.). A single collection from splash pools on Green Island, near Resolution.

Cristatella mucedo Cuv. Five collections from Yellowknife Bay east to McLeod Bay at depths of 0.3 to 4.5 metres.

These four species are all of widespread distribution, occurring in North America, Europe and Asia.

Turbellaria

Several planarians were collected in dredgings at depths of one to eight metres. They appeared to be of the genus *Dugesia,* but were not suitably preserved for species identification.

Nematoda

The free-living nematodes were submitted to Dr. L. J. Thomas of the University of Illinois who reports the following genera.

Aphelenchus sp. Found in the deep water of Christie Bay, 400-500 metres.

Dorylaimus spp. Many collections at various depths down to 400 metres.

Doryllium sp. Few specimens at moderate depths.

Gordius sp. Common in shallow water.

Hydromermis sp. One specimen at 200 metres.

Paragordius sp. Several specimens in shallow water.

Oligochaeta

The oligochaete worms have been examined by Dr. S. A. Cain of Oxford University, who reports five genera, one of which is represented by at least three species. It is unfortunate that the Tubificidae of the deeper water were not suitably preserved for specific determination.

Lumbriculus sp. A large species in shallow water at Burnt and Outpost Islands.

Lumbriculus inconstans (F. Smith). Shallow water at Yellowknife Bay and Outpost Island.

Lumbriculus variegatus (O. F. Müller). Water's edge at Snowdrift and Outpost Islands.

Mesoporodrilus sp. Common in all parts of the lake at depths of 20 to 75 metres.

Limnodrilus, probably *claparedeianus* Ratzel. Frequent at depths of 5 to 25 metres.

Limnodrilus sp. or spp. Common at moderate depths.

Tubifex spp. Common at all depths. Specimens from the deepest water appear to be of a single species.

Hirudinea

The following leeches have been identified by Dr. J. P. Moore of the University of Pennsylvania.

Glossiphonia complanata (L.). Common in shallows at Yellowknife Bay and off Hay River.

Helobdella stagnalis (L.). Yellowknife Bay and Outpost Island.

Helobdella fusca (Castle). Green Island, west of Resolution.

Piscicola milneri Verrill. Very common at Resolution and in other localities around main lake.

Haemopis marmoratus (Say). Gros Cap.

Erpobdella punctata (Leidy). Common in Yellowknife Bay.

Erpobdella atomaria (Carena). Several specimens from Outpost Island. Dr. Moore remarks that this is a new record for North America although the species is very common in Europe.

Nephelopsis obscura Verrill. Caribou Island southeast of Gros Cap.

Ostracoda

The ostracods have been identified by Dr. W. L. Tressler of College Park, Maryland. He reports three widespread species and two others, apparently new, which he proposes to describe after further study.

Cypriconcha barbata (Forbes). Collected only at Yellowknife in 3 to 6 metres of water.

Candona crogmaniana Turner. This was the most abundant species. It was found in all parts of the lake and from depths of 5 to 150 metres.

Candona decora Furtos. Less abundant but even more widespread than the previous species. *C. decora* was the only ostracod found between 150 and 600 metres.

Candona (nov. sp.?). Common in the shallow water near Resolution and elsewhere in the main lake. Not taken in the East Arm.

Limnocythere (nov. sp.?). A few specimens from shallow water near the Taltson River and Preble Island.

Mysidaceae

Mysis relicta Loven. Abundant in Great Slave in both shallow and deep water. Larkin (1948) has published a full account of the life history and ecology of this important species.

Amphipoda

Gammarus limnaeus Smith. This large amphipod was taken in moderate numbers in dredgings in the upper ten metres. It was also common in the stomachs of several fish species.

Hyalella azteca (Saussure). This species was common only in shallow protected bays. In colder and more exposed locations *Pontoporeia* was the dominant amphipod right up to shore.

Pontoporeia affinis Lindstrom. This species, by far the most important organism in the bottom fauna, has been reported on by Larkin (1948).

Insecta

Large numbers of adult aquatic insects of seven orders have been collected at Great Slave Lake and identified by appropriate systematists. The larval and nymphal stages taken in dredgings were not numerous except in the Tendipedidae. Since time was not available for rearing studies, few of the larval forms have been identified to species. Moreover, the large majority of the adults collected are part of a shallow-water "shore" fauna rather than of the open-water bottom fauna with which this report is concerned. It has therefore been decided to reserve for publication elsewhere the rather extensive lists of aquatic insects,

mentioning here only those forms taken in the dredging samples at depths of not less than one metre.

In this group only four orders are represented.

PLECOPTERA

Isogenus frontalis Newman.

Isoperla decolorata (Walker).

Nymphs of these species, identified by Dr. W. E. Ricker, of Nanaimo, B.C. were found at depths down to six metres in wave-washed localities. Adults of four additional species were collected at the lake and were probably breeding in it.

Pteronarcys dorsata (Say). In the Hearne Channel.

Nemoura arctica Esben-Petersen. Hearne Channel and Pearson Point.

Capnia nearctica Banks. Whaleback Islands.

Arcynopteryx compacta MacLachlan. From the Hearne Channel, Slave River Delta, Egg Island and Pearson Point.

EPHEMEROPTERA

Hexagenia occulta Walker.

Ephemera simulans Walker.

Nymphs of these species, identified by Dr. F. P. Ide, University of Toronto, were common in depths down to four metres in Yellowknife Bay and at Brabant Island, near the outlet of the lake.

TRICHOPTERA

Adults of 49 species of caddis have been identified by Dr. H. H. Ross of the State Natural History Survey, Urbana, Illinois. For the larval material, taken in dredgings, identification is possible to family and in some instances to genus as in the following list.

Hydropsyche, probably *separata* Banks. Larvae in dredgings near Resolution and Big Island.

Hydroptilidae. Larvae near Big Island.

Phryganeidae. Larvae from Yellowknife Bay.

Agrypnia sp. Larvae from McLeod Bay near Reliance.

Limnephilidae. Larvae from Yellowknife Bay, Gros Cap, Outpost Island.

Limnephilus spp. From Hay River and Outpost Island.

Molanna flavicornis Bks. Yellowknife and McLeod Bays.

Arthripsodes sp. Green Island, west of Resolution and Yellowknife Bay.

The above larvae were collected mostly from 1 to 10 metres with a few specimens at 13 metres. Only empty cases were found at greater depths.

DIPTERA

TENDIPEDIDAE (CHIRONOMIDAE). The Chironomid larvae were sorted into genera under the direction of Dr. J. G. Rempel, University of Saskatchewan.

The subfamily Tanypodinae was represented by several species of the genera *Pentaneura* and *Procladius*. These were taken in shallow water, less than 20 metres in depth.

The subfamily Orthocladiinae was represented by several species of the genus *Spaniotoma*.

Within the subfamily Chironominae the genus *Chironomus* was represented by several species belonging to the subgenus *Chironomus* and others to the subgenus *Cryptochironomus*. The genus *Tanytarsus* was represented by members of the *inermipes* group. The Chironominae were found in shallow to middle depths, rarely more than 50 metres.

A more detailed examination was made of the deep-water forms which were all of the genus *Spaniotoma*. Although species identification could only be made by rearing, Dr. Rempel was able to distinguish three well-defined species. Of these the first was found to occur down to a depth of 58 metres. The second was collected from 17 to 128 metres. The third was the only species in the very deep water. It was collected in large numbers at all depths from 36 to 540 metres.

Hydracarina

The hydrachnids have been identified by Mr. David Cook of the University of Michigan.

Eylais sp. One specimen from Outpost Island.

Hydrachna cruenta (Müll). Several from Outpost Island.

Lebertia porosa Thor. This was the most numerous and widespread species in our collections. Common at Pearson Point, Yellowknife Bay and near the outlet of the lake. More than 200 specimens were taken from the stomach of one round whitefish *(Prosopium cylindraceum)*.

Hygrobates sp. Partly digested in a fish stomach.

Unionicola crassipes (Müll.) One specimen near Fort Rae.

Piona interrupta Mar. Several collections.

Arrenurus sp. One specimen from Outpost Island.

Gastropoda

Extensive collections of aquatic snails were identified by Dr. J. G. Oughton, now of the Ontario Agricultural College, Guelph.

Valvata sincera Say. This is the most abundant gastropod in Great Slave Lake. About 190 specimens were taken from 50 dredgings in various parts of the lake.

Amnicola binneyana (Hannibal). Common along the south shore of the main lake and north of the Taltson River.

Stagnicola catoscopium (Say). From the Outpost Islands and the Hearne Channel east of Gros Cap.

Stagnicola caperata (Say). At Pearson Point.

Fossaria, cf. *obrussa* (Say). Big Island near the outlet of the lake.

Menetus exacuous (Say). Big Island near the outlet of the lake.

Gyraulus parvus (Say). Common in all parts of the lake including Yellowknife, Big Island, Resolution and Reliance. Dr. Oughton notes that these specimens are unlike typical *G. parvus* in having a more rounded base.

Gyraulus hirsutus (Gould). At Yellowknife and Big Island but much less common than the *G. parvus*.

Physa, cf. *gyrina* Say. At Yellowknife Bay and Pearson Point.

The majority of these gastropods were taken from depths of less than 7 metres with smaller numbers down to 12 and a few *Valvata* and *Amnicola* down to 17 metres.

Pelecypoda

The Sphaeriidae of Great Slave Lake have been the subject of a detailed study and published account by Herrington (1950). He records the following sixteen species: *Pisidium conventus* Clessin, *P. subtruncatum* Malm., *P. idahoense* Roper, *P. lilljeborgi* Clessin, *P. medianum* Sterki, *P. pauperculum* Sterki, *P. compressum* Prime, *P. punctatum* Sterki, *P. fallax* Sterki, *P. lermondi* Sterki, *P. milium* Held., *Sphaerium striatinum* Lamark, *S. tenue nitidum* Clessin, *Musculium transversum* Say, *M. winkleyi* Sterki, *M. ryckholti* Normand.

The two first mentioned species, *P. conventus* and *P. subtruncatum*, far outnumbered the remaining species. *P. conventus* was the most widespread and occurred at depths down to 219 metres.

Two large freshwater mussels were collected from Great Slave Lake.

Lampsilis siliquoidea Barnes. Common in the shallows near the inlets of the Hay, Big Buffalo and Talston Rivers. Occasional specimens were found near Resolution and in Frank Channel three miles south of Fort Rae. Dr. Oughton reports that in some respects the specimens taken were intermediate between *L. siliquoidea* and *L. radiata*.

Anodonta kennicotti Lea. Also found at the mouth of the Hay River and in Frank Channel.

COMPOSITION AND DEPTH DISTRIBUTION OF THE BOTTOM POPULATION

A broad picture of the composition of the bottom population can be obtained by combining the data from all parts of the lake. Thus in Table I, the total numbers of the various groups of bottom organisms are listed and calculations made to show their averages per unit area and their percentage contributions to the total population. Differences in the composition and

TABLE I. Summary of bottom organisms collected in 590 dredgings in Great Slave Lake, 1944-1947.

Organisms	Total number collected	Average number per square metre	Percentage of population
Amphipoda	30,044	1018	62.5
Sphaeriidae	5,162	175	10.8
Oligochaeta	4,846	164	10.1
Chironomid larvae	3,688	125	7.7
Ostracoda	1,697	57	3.5
Gastropoda	1,426	48	2.9
Nematoda	710	24	1.5
Miscellaneous	468	16	1.0
All organisms	48,041	1627	100.0

distribution of populations in the various regions of the lake will be considered in a later section.

It will be seen from Table I that the amphipods constitute more than 60 per cent of the numbers of the total population. Larkin (1948) has shown also that *Pontoporeia*, the chief amphipod present, makes up almost 70 per cent of the total weight. Of the remaining organisms, the sphaeriids and oligochaetes each contribute about 10 per cent (numerically), the chironomid larvae nearly 8 per cent, the ostracods, gastropods, nematodes from 3.5 to 1.5 per cent. The organisms listed as miscellaneous included *Mysis*, caddis larvae, mayfly nymphs, dipterous larvae other than chironomids, planaria, hydrachnids, stoneflies and leeches, in decreasing order of abundance. The value 1,627 organisms per square metre is simply the average from all the dredgings taken. It should be weighted according to the depth distribution, and as will be seen later, according to major differences in the density of the bottom population in different regions of the lake.

The depth distribution of organisms in the whole lake is indicated in Table II, which shows the number of dredgings in each depth range, the numbers of organisms of the seven major groups, the total number and the total

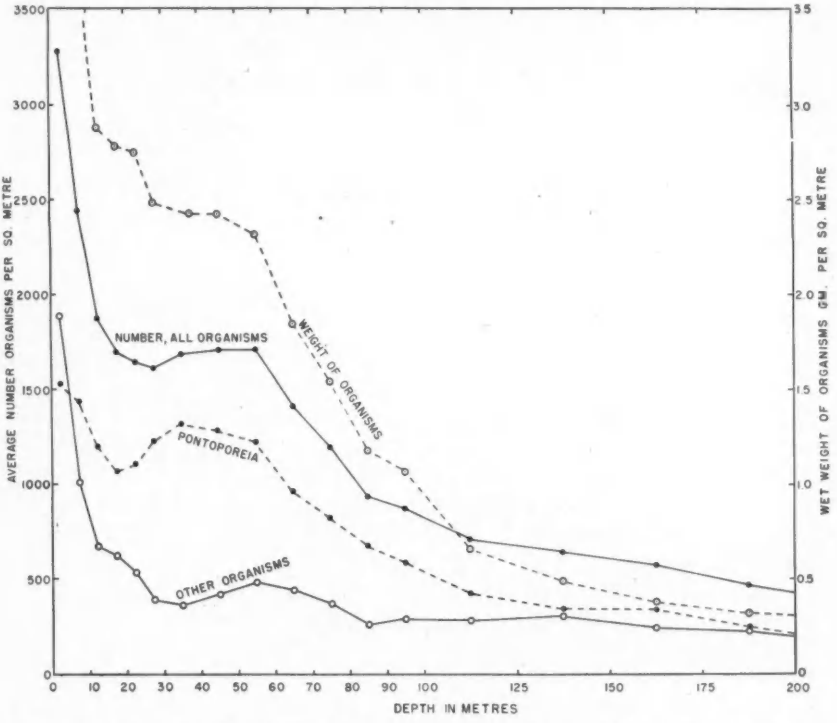

FIGURE 5. Numerical distribution of bottom organisms from 0 to 200 metres in Great Slave Lake, curves smoothed by threes.

TABLE II. Average numbers of various groups of organisms per square metre and combined weight of organisms at all depths in Great Slave Lake.

Depth range	Number of dredgings	Amphipods	Sphaeriids	Oligochaetes	Chironomid larvae	Ostracods	Gastropods	Nematodes	Miscellaneous	All organisms	Weight
metres											*g./m.²*
0–5	69	1530	636	296	402	26	348	4	49	3291	9.68
5–10	60	1476	300	112	104	44	64	5	16	2121	2.86
10–15	64	1310	280	214	96	56	68	18	6	2042	2.90
15–20	38	820	212	336	110	71	4	3	2	1558	2.88
20–25	44	1088	111	224	92	59	1	2	3	1581	2.56
25–30	27	1442	91	125	91	52	2	12	5	1817	2.80
30–40	37	1144	79	49	109	81	0	2	5	1471	2.10
40–50	18	1382	55	77	113	152	0	7	2	1790	2.38
50–60	38	1324	33	242	116	98	1	2	5	1869	2.80
60–70	23	974	36	143	111	20	0	15	5	1483	1.81
70–80	25	602	25	55	103	66	1	41	11	903	.93
80–90	15	904	27	147	95	36	0	16	5	1229	1.89
90–100	16	512	11	41	85	40	0	4	1	695	.71
100–125	23	352	17	76	125	36	0	112	0	718	.62
125–150	11	404	11	185	42	25	0	53	0	720	.56
150–175	11	286	9	45	34	11	0	122	0	507	.31
175–200	6	300	1	52	27	63	0	53	0	496	.27
200–300	25	140	2	126	20	18	0	80	0	386	.39
300–400	12	150	0	46	4	4	0	96	0	300	.23
400–500	12	176	0	40	2	6	0	30	0	254	.15
500–600	16	208	0	78	4	12	0	100	0	402	.34

wet weight of organisms per square metre. The meaning of these data can be seen more clearly with the help of graphs, Figures 5 and 6, which show distributions down to 200 metres. The bottom population in the very deep water, 200-600 metres, is considered in a later section and plotted in Figure 9.

The average weight of bottom organisms, as shown in Figure 5, falls rapidly from a maximum of 9.68 gm. per sq. m. in the 0- to 5-metre zone to 2.8 gm. at 5-10 metres, then rather gradually to about 2.3 gm. at 60 metres. From this point it again declines quickly to about 0.5 gm. at 125 metres, then more slowly into the very deep water where it maintains an average of about 0.3 gm. The curve for total numbers begins with a maximum in shallow water of 3,291 per sq. m. and follows the same trend as that for weight. However, in the region from 30 to 60 metres there is a slight increase over the numbers at 25 to 30 metres. The average number of organisms at 200 metres is about 400 per sq. m. and again this is maintained into the deep water. Since *Pontoporeia* is the dominant bottom organism, its depth distribution is plotted in Figure 5 and, for comparison, the numbers of all other organisms at corresponding depths. It is of interest that *Pontoporeia*, usually thought of as a cold stenotherm species, should be present in large numbers in the upper five metres of the lake. This is not surprising when it is noted that the temperatures in this stratum are usually less than 11°C. at midsummer. The numbers of *Pontoporeia* decline from 1,530 in 0-5 metres to 820 at 15-20 metres, then increase again to 1,442 at 25-30 metres. The decrease at 15 to 20 metres is suggestive of the sublittoral minimum frequently observed in the depth distribution of bottom organisms. It was not observed for any other of the groups of organisms in Great Slave Lake, although the chironomid larvae, Figure 6, show a slight suggestion of this feature. *Pontoporeia* is widely distributed in the deep water, where its numbers usually run from 200 to 400 per sq. m.

The depth distribution of all groups of organisms other than *Pontoporeia* have been plotted in another graph, Figure 6. Sphaeriids, mainly *Pisidium* of three species, show a remarkably uniform depth distribution. From a maximum of 636 per sq. m. in the 0- to 5-metre zone the numbers fall off rapidly to 100 at 35 m. and then more slowly to about 15 per sq. m. at 100 metres. From this point they fade away toward the very deep water, the greatest depth from which they were collected being 264 metres. Details of distribution of the species of sphaeriids in Great Slave Lake have been recorded by Herrington (1950).

Oligochaete depth distribution is rather irregular, with apparent minima at 5 to 10, 30 to 40 and 80 to 90 metres. It should be noted that minor variations, especially in the less numerous organisms, may be apparent, i.e. the result of insufficient sampling, rather than real. The average number of oligochaetes is considerable, making up 10 per cent of the population and continuing from 100 metres in fairly constant numbers into the deepest water. Chironomid larvae show the above-mentioned suggestion of a sublittoral minimum and decline to almost negligible numbers below 300 metres. Ostracods are few in the shallow water, increase to a maximum of 110 per sq. m. between 40 and 50 metres, then decline to an average of about 25 in the deep water. The gastropods show a

maximum of 348 per sq. m. in the shallow water and like the sphaeriids, decline rapidly with increasing depth. They are rare below 25 metres, and the deepest living specimens were taken at 55 metres. The nematodes were the only group of organisms consistently more abundant in the deeper water. From shore to 50 metres they averaged about 7 per sq. m. then they increased gradually to about 100 at 100 metres and averaged about 80 per sq. m. in the deepest water.

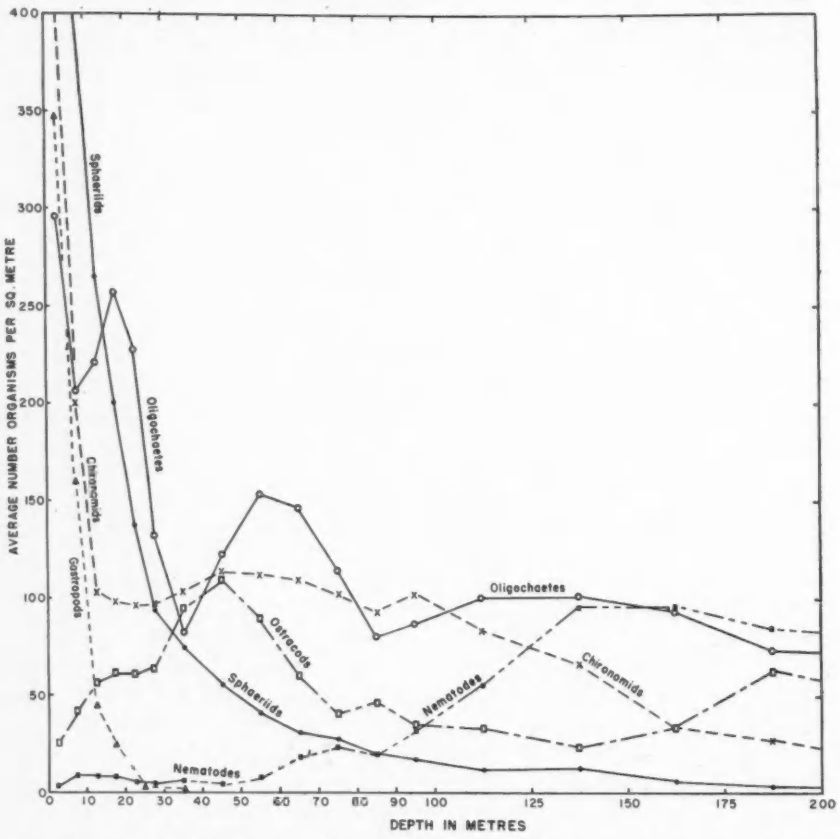

FIGURE 6. Details of depth distribution of groups of bottom organisms other than *Pontoporeia* in Great Slave Lake, curves smoothed by threes.

REGIONAL DIFFERENCES IN THE BOTTOM POPULATION

In a lake so large and with such varied regions as Great Slave, it would seem probable that the bottom fauna would differ in quality, quantity and distribution in the various areas. The degree of variation between areas is of ecological interest and of special significance as an indication of the validity of the "average"

TABLE III. Depth distribution of bottom organisms expressed in numbers and weight, per square metre, in five divisions of Great Slave Lake.

Depth zone	Main lake			Yellowknife Bay			Islands area			Christie and Wildbread Bays			McLeod Bay		
	No. dredgings	Av. no. organisms	Av. wt.	No. dredgings	Av. no. organisms	Av. wt.	No. dredgings	Av. no. organisms	Av. wt.	No. dredgings	Av. no. organisms	Av. wt.	No. dredgings	Av. no. organisms	Av. wt.
metres			g.			g.			g.			g.			g.
0–5	36	1430	3.28	13	4080	8.86	19	4080	14.30	8	9540	20.14	2	460	1.32
5–10	32	1610	1.94	9	2180	4.34	11	3360	5.26	3	3320	4.38	0	—	—
10–15	33	1860	3.00	10	3080	4.14	11	2020	3.40	5	720	1.24	0	—	—
15–20	17	2340	3.04	7	2860	4.74	5	700	1.26	4	3220	4.56	0	—	—
20–25	21	1850	3.06	4	2600	5.10	14	1140	1.62	1	1760	1.70	2	1060	1.50
25–30	19	1995	3.78	1	2720	7.76	3	2200	2.26	0	—	—	0	—	—
30–40	16	1640	2.62	1	1680	3.96	14	1080	1.18	5	1680	1.98	2	1180	1.54
40–50	8	1790	3.80	0	—	—	4	1020	1.16	2	2540	3.76	1	780	.86
50–60	22	2040	2.94	2	2740	3.80	10	1440	1.90	5	2100	2.80	2	400	.36
60–70	9	1440	2.28	2	4080	2.98	4	1840	1.66	8	840	1.00	1	200	.36
70–80	3	880	1.76				9	960	1.24	14	660	.34	2	740	1.32
80–90	2	2120	1.60				7	1240	1.50	4	740	.40	1	460	.30
90–100	5	1040	1.00				5	620	.98	2	260	.36	3	360	.22
100–125	4	1180	1.04				7	680	.84	14	500	.24	6	440	.32
125–150	1	1820	1.80				6	660	.50	4	420	.32	1	360	.26
150–175	1	400	4.80				2	460	.44	7	480	.28	3	480	.20
175–200	0	—	—				2	800	.16	6	280	.18	4	300	.34

TABLE IV. Percentage composition, by numbers, of the bottom organisms at all depths in five regions of Great Slave Lake.

	Whole lake	Main lake	Yellowknife Bay	The Islands	Christie and Wildbread Bays	McLeod Bay
Amphipods	62.5	72.1	55.1	61.0	49.7	48.5
Sphaeriids	10.8	5.5	18.6	13.2	12.9	5.9
Oligochaetes	10.1	12.2	9.0	6.0	15.8	1.9
Chironomids	7.7	4.2	9.0	8.9	11.4	24.8
Ostracods	3.5	3.8	3.4	4.2	0.7	5.0
Gastropods	2.9	0.8	4.1	5.0	4.6	1.6
Nematodes	1.5	0.4	0.3	0.7	4.5	8.5
Miscellaneous	1.0	1.1	0.5	1.0	0.4	3.8

distribution of organisms presented above. In the first analysis of the dredging data, the lake was divided into eight parts. These parts and the number of dredgings taken in each were listed above, page 489. For each of the eight areas there was calculated the average number of organisms at each depth and the depth distribution of each group of organisms. It was then apparent that some of the adjacent divisions had similar faunal composition and distribution. Since the Resolution and North Arm areas resembled the main lake, these three were combined. For the same reason, the Outpost and Gros Cap area was merged with the "Islands" region. This left five areas for which comparative data are given in Tables III and IV.

The numbers and weights of organisms found at various depths in the five divisions of the lake are indicated in Table III. These values are plotted in Figure 7, for numbers, and Figure 8, for weights. In each case, the curves are smoothed by threes to emphasize trends and subdue erratic variations. The curves for the main lake based on 230 dredgings may be used as a basis for comparison. Yellowknife Bay stands out in both graphs as having about one-third larger numbers and greater weight of organisms than are found at similar depths in the main lake. The Islands area has slightly larger numbers and weights about equal to those of the main lake. The population of the upper 50 metres of Christie Bay is equal to or greater than that of the main lake, and in the deep water its numbers are two-thirds and its weight about one-third those of the main lake. The Islands area has less population in the upper 50 metres than Christie Bay but considerably more at depths of from 50 to 150 metres. McLeod Bay

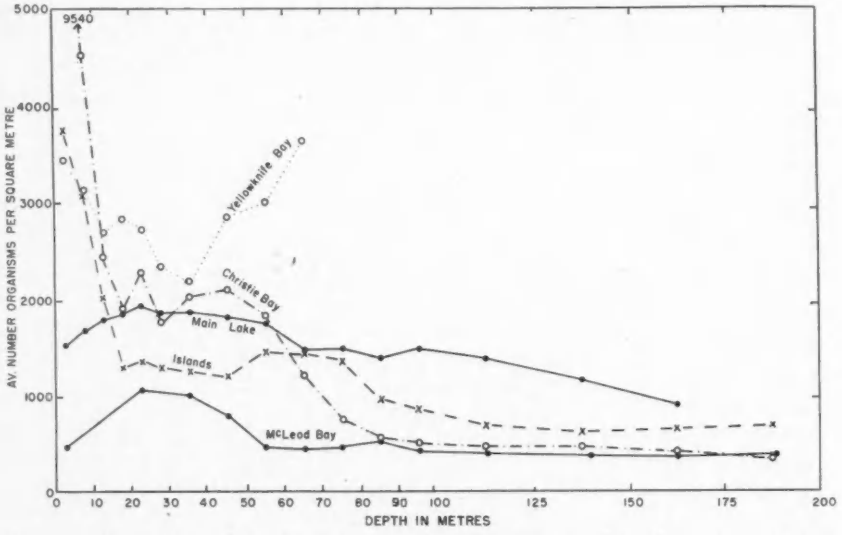

FIGURE 7. Numerical distribution of bottom organisms with depth in five regions of Great Slave Lake, curves smoothed by threes.

has the smallest numbers and least weight of organisms of the five divisions. This was to be expected, since its physical conditions and fish population had already indicated extreme oligotrophy (Rawson, 1950, 1951a).

It is of interest to learn whether the above-mentioned differences in quantity of bottom organisms in the five areas are accompanied by differences in composition. Table IV shows the percentage of each of the main groups of organisms found in samples from all depths in the five areas and in the whole lake. In the main lake, amphipods are about 10 per cent above the average for the whole lake, but the main lake is low in molluscs and nematodes. Yellowknife Bay has the greatest number of sphaeriids. The composition of the bottom population in the Islands area is much like the general average. Christie and McLeod Bays have fewer amphipods and more chironomids than the main lake. The chironomids comprise about one-quarter of the bottom population of McLeod and Christie Bays. This does not indicate an absolute increase in chironomid larvae as compared to the main lake, but a relative increase, because the numbers of other organisms are very low.

The analysis in Table IV is based on the total organisms collected in each division of the lake. It takes no account of the fact that these divisions have different proportions of very deep water, nor of the situation that the number of dredgings is not uniform in the various depth zones, see Table III. For these reasons a further analysis was made using the averages rather than totals of

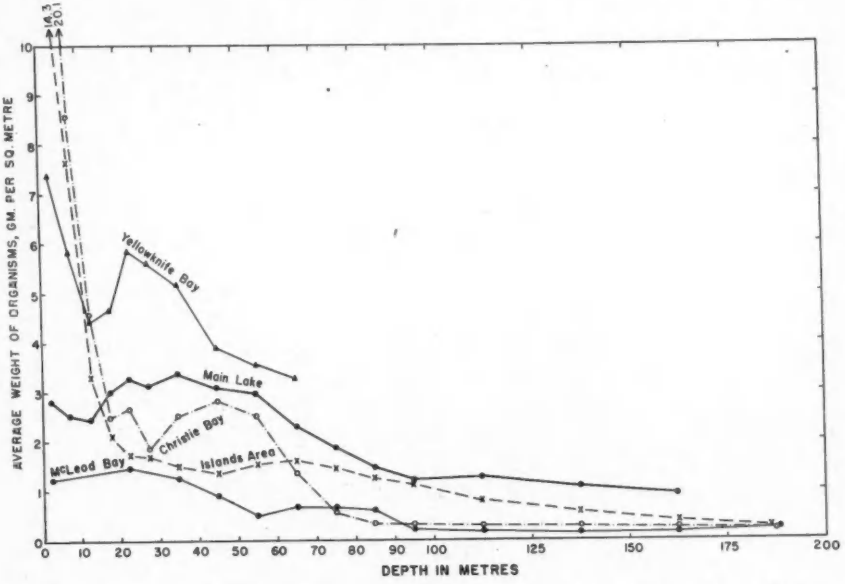

FIGURE 8. Gravimetric distribution of bottom organisms with depth in five regions of Great Slave Lake, curves smoothed by threes.

organisms and comparing the composition in different areas at similar depths. By this means the figures given in Table IV for the main lake, Yellowknife Bay and the Islands were found to be representative of these areas. However, in Christie and McLeod Bays, amphipods are relatively more abundant and nematodes less abundant than is indicated by the values in Table IV.

The average numbers and weights of organisms at all depths in the five divisions were presented in Table III. The percentage of the area of each division made up by each depth zone was presented in an earlier paper (Rawson, 1951a, Table II). By combining these data, it is possible to calculate a true average for numbers and weights of organisms in each division. This has been done in Table V. A further step was to calculate an average for the whole lake, weighting the values for the different divisions according to their relative areas. Yellowknife Bay is the richest of the five areas, with 70 per cent greater numbers and double the weight of organisms in the main lake. Yellowknife Bay is somewhat divided from the main lake by the east and west Mirage Islands, and being shallower than the other divisions, apparently acts like a smaller and therefore richer lake. The Islands area is also slightly richer than the main lake. Christie Bay has about three-fifths the numbers and less than half the weight of organisms in the main lake, while McLeod Bay is by far the lowest with less than one-third the numbers and one-fifth of the weight. In view of this diversity in the amount of bottom organisms in different parts of the lake, the significance of an average for the whole lake is somewhat questionable. However, the values for the whole lake resemble those for the main lake, since the latter comprises 75 per cent of the total water area. Also, the richer Yellowknife Bay and Islands areas tend to compensate for the very poor bottom population of Christie and McLeod Bays. Thus the final value of 1,603 organisms and 2.49 grams per square metre is a reasonable approximation for the whole lake.

TABLE V. Average numbers and weights of bottom organisms in each of the five divisions, and weighted average for the whole of Great Slave Lake.

	Area	Mean depth	Average number organisms per sq. m.	Average weight of organisms	Equivalent dry weight
	sq. km.	*m.*	*no./sq. m.*	*g./sq. m.*	*kg./ha.*
Main lake	19,170	41	1,706	2.69	4.0
Yellowknife Bay	230	26	2,894	5.19	7.8
Islands area	2,290	76	1,988	3.53	5.3
Christie and adjacent bays	2,120	199	1,061	1.17	1.7
McLeod Bay	1,590	120	487	0.48	0.72
Whole lake	25,400	62	1,603	2.49	3.7

THE BOTTOM FAUNA AT GREAT DEPTHS

The large basin which dips down to 614 metres in the east arm of Great Slave Lake is of unusual interest since few lakes on this continent approach this

depth. The maximum recorded for Great Bear Lake is 400+ m., Lake Superior 393 m., and Lake Michigan 281 m. With the exception of Eggleton's (1937) work on Lake Michigan, the bottom fauna of very deep lakes in North America is practically unknown. Our investigating party spent some time, chiefly in 1946, using equipment specially designed for dredging in this area (Rawson, 1947b).

The depth of 200 metres has been chosen arbitrarily as a convenient upper limit for our area of great depths. This decision was based on the observation that at 200 metres the bottom animals had decreased to a thin but rather constant population which continued down to 600 metres. Also, with few exceptions, species found as deep as 200 metres continued down to 600. This region of great depth might be called abyssal, but the term has been avoided because of lack of agreement on its use. In Lake Baikal that part below 300 metres has been called abyssal (Brooks, 1950). Naumann (1931) indicated that, in limnology, abyssal was used only for depths greater than 600 metres. Marine biologists use 200 metres as an arbitrary division between the sublittoral and deep-sea systems, and 1,000 metres as the upper limit of the abyssal zone. However, as Sverdrup (1942) points out, the natural boundaries of these zones vary in different regions.

The largest area in Great Slave Lake deeper than 200 metres is in Christie Bay, Figure 4. An area of 854 sq. km. (328 sq. mi.), which is more than half the total area of Christie Bay, exceeds 200 metres in depth. In McLeod Bay about 235 sq. km. (91 sq. mi.) exceed 200 metres, and in the Hearne Channel, Figure 3, 338 sq. km. (131 sq. mi.). Thus the total area deeper than 200 metres is 1,427 sq. km. (550 sq. mi.) or about 7.3 per cent of the area of the lake. In these deep regions, 65 dredgings were taken, most of them (49) in Christie Bay. The physical conditions at depths of 200 to 600 metres have been described in a previous paper (Rawson, 1950) from which a few essential data may be quoted. At 200 metres the temperature was never higher than 4°C. and at 600 metres it was as low as 3.6°C. Dissolved oxygen varied from 10.4 to 12.0 mg. per litre and was never less than 81 per cent of saturation. The hydrogen ion concentration varied between pH 7.5 and 7.7, and the mineral content was the same as that of the surface water. The bottom deposits in the deepest water are a fine-grained, grey clay of creamy consistency at the surface and stiffer below. Organic material is present in the surface layer in very minute quantities. A sample from a depth of 575 metres was analysed for particle size through the kindness of the Geological Survey of Canada, Ottawa. The results indicate an extremely fine-grained material.

Sand grains, diameter greater than 0.1 mm. were very scarce.

Silt particles, diameter 0.01 to 0.1 mm. made up less than 2 per cent of the sample.

Clay particles, diameter 0.001 to 0.01 mm. made up about 40 per cent of the sample.

Clay particles, of diameters less than .001 mm. made up the remaining 58 per cent.

Minute amounts of carbonaceous plant material were found, but no diatoms, pollen grains or microfauna.

The depth distribution of bottom organisms taken in the deep-water dredgings was indicated in Table II above. These data have been plotted in the graph, Figure 9, together with comparative data for the adjacent depths, 150 to 200 metres. *Pontoporeia affinis* is the dominant organism, averaging about 185 per square metre. Nematodes and oligochaetes are next and nearly equal in numbers, averaging about 70 per sq. m. Ostracods and chironomid larvae each

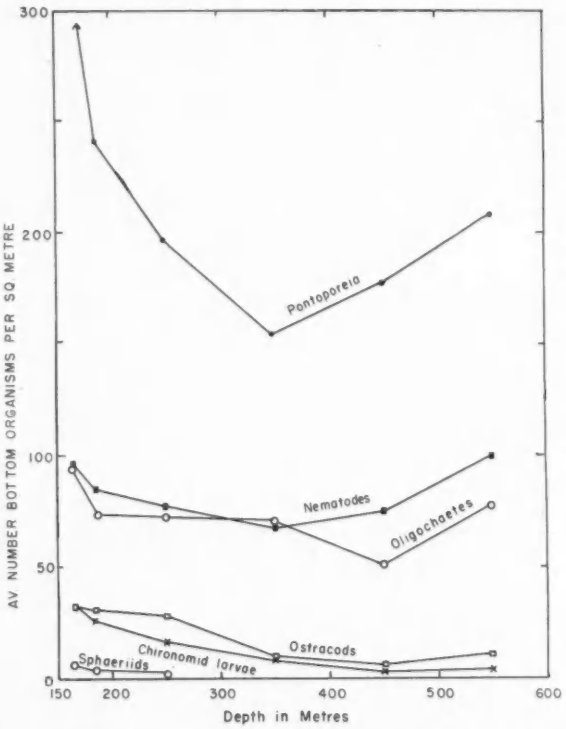

FIGURE 9. Numerical distribution of bottom organisms in the very deep water of Great Slave Lake.

average about 15 per sq. m., but drop off to less than 10 in the deepest water. Sphaeriids are present in minute numbers between 200 and 300 metres, but none were found in the deeper dredgings. The thin population of this region is remarkable for its constancy. Each group of organisms persists into the deepest water and most of them show a slight increase in the lowest 100 metres. Since only 16 dredgings were taken in this lowest zone, the apparent increase may be an accident of sampling. The average number of all organisms in the 200- to 600-metre area is about 310, and the average weight 0.28 grams per square metre.

Special care was taken in the identification of organisms from the great depths. It appears that each group is represented by a single species.

Amphipoda	– *Pontoporeia affinis*
Ostracoda	– *Candona decora*
Nematoda	– *Hydromermis* sp.
Oligochaeta	– *Tubifex* sp.
Chironomidae	– *Spaniotoma* sp.
Sphaeriidae	– *Pisidium abortivum*

The list of six species is the more striking when it is noted that they represent four phyla and six classes. Such paucity of species in a recent "post-glacial" lake is to be contrasted to the large number of species and species swarms observed in the depths of ancient lakes such as Baikal and Tanganyika (Hesse, 1937; Brooks, 1950).

THE INFLUENCE OF THE SLAVE RIVER DELTA

The Slave River enters Great Slave Lake from the south with a mean annual inflow averaging 118,000 cu. ft. per sec. (3,540 cu. m./sec.). The magnitude of this inflow is difficult to comprehend, and one is more impressed to learn that it carries into the lake a daily quota of 54,500 metric tons (60,000 tons avoir.) of dissolved materials, plus an additional daily burden of about 36,000 metric tons of suspended silt during the summer months (Rawson, 1950). Although the lake is young, the delta has already pushed well out beyond the original shoreline, and vast bars provide evidence of the current-building process. Flying out over the lake one can frequently see a distinct margin of the muddy water from 10 to 40 miles (16 to 64 km.) out from shore. Some account of transparency, temperature and dissolved oxygen in the delta region was provided in a report on the physical limnology of the lake (Rawson, 1950). A preliminary attempt to determine the biological effect of these delta conditions led to a comparison of the bottom population close to the river mouth with that of similar depths in other portions of the main lake.

The delta area was arbitrarily defined as a zone about 25 km. (16 miles) in width, bounded on the west by a line from Resolution to Egg Island and on the east by a line from Stony Island toward the west end of the Outpost Islands, Figure 2. The area enclosed by these boundaries is approximately 1,250 sq. km. (480 sq. mi.). Within this area, 43 dredgings were taken at depths down to 105 metres. It was soon evident that the muddy delta region was more heavily populated than the clear water regions of the main lake.

An analysis of the dredging data from the delta area and a comparison with those from the main lake are presented in Table VI. The average number of organisms per square metre off the delta is 2,329, an excess of 51 per cent over that of similar depths in the main lake. The weight of organisms off the delta is 3.29 g. per sq. m., an excess of 32 per cent over the main lake. The graph, Figure 10, shows that most of this increase in numbers is in the upper 50 metres, and that the population at depths of 50 to 100 metres is nearly equal to that of the main lake. The average values for numbers of organisms off the delta between 50 and 70 metres fall below the corresponding averages for the main

lake, but this is not considered significant because of the small number of dredgings taken in that part of the delta area.

TABLE VI. Comparison of average numbers and wet weights of organisms per square metre at depths of 0 to 100 metres in the Delta region and in the main part of Great Slave Lake.

Organism	Main lake	Delta	Percentage difference
Amphipoda	1,132	1,416	+ 25
Sphaeriidae	73	46	− 37
Oligochaeta	162	726	+ 350
Chironomid larvae	74	92	+ 24
Ostracoda	65	21	− 68
Gastropoda	11	0	− 100
Nematoda	5	19	+ 270
Miscellaneous	17	8	− 53
All organisms	1,539	2,328	+ 51
Total weight (grams)	2.50	3.29	+ 32

The greater part of the increase in numbers of bottom organisms off the delta is due to the oligochaetes, which were about 4.5 times as numerous in this region as in the main lake. Presumably this group found favourable living conditions in the rapidly accumulating delta deposits. The only other group which showed obvious increase in the delta region was the nematodes which were 3.5 times as numerous here as in the main lake. Other groups of organisms were substantially fewer in the delta area, the sphaeriids by 37 per cent, ostracods by 68 per cent, and the gastropods were absent from the samples taken.

The increase in oligochaetes, which are not much used as food by fish, and the decrease in mollusca, which are greatly used, would suggest that delta conditions have a deleterious effect on the production of fish food. It should

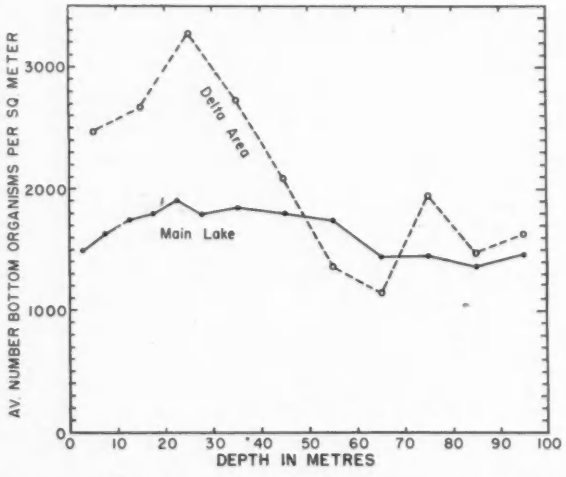

FIGURE 10. Comparison of the average number of bottom organisms in the delta region and in the main part of Great Slave Lake.

be pointed out, however, that heavy catches of commercial fish were made in gill nets set in very muddy parts of the delta region (Rawson, 1951a).

While the bottom population of the delta exceeds that of the main lake, it is not so great as that of Yellowknife Bay, Table III and Figure 7. In the upper 50 metres, the average number of organisms per square metre in Yellowknife Bay is 2,743 and off the delta, 2,660. The average weights of organisms in grams per sq. m. are 5.56 and 4.62, respectively. It is of interest that these two regions, in which the bottom population greatly exceeds that of any other part of the lake, should be areas affected by direct inflow of rivers. It is conceivable that the observed increase in the bottom fauna might be due to the direct fertilizing effect of organic and inorganic materials carried in by the rivers, or to the effect of the rivers in raising water temperatures, or to both. The temperatures at depths of 25 to 50 metres in Yellowknife Bay and off the Slave delta show the effects of warming by river water (Rawson, 1950).

BOTTOM ORGANISMS AS FISH FOOD

One of the reasons for studying the bottom fauna was to assess its contribution to the production of fish in the lake. About 12,000 specimens representing the 12 major species of fish in the lake were taken in the program of gill-net sampling. The stomach contents of most of these specimens were examined and the resulting information has been reported (Rawson, 1951a). Other references to the role of bottom fauna in production of fish in Great Slave Lake have been made by Rawson (1947a, 1949) and by Larkin (1948). Since the information is published in several reports, it is considered desirable to draw together the general picture of utilization of bottom foods by the fish of Great Slave Lake.

A summary of the amounts of bottom foods used by the major species of fish has been drawn from the published papers referred to above and from the original field records. The results, in Table VII, are expressed as average percentage volumes rather than numbers of food organisms or frequency of occurrence. Four species of fish stand out as depending almost entirely on bottom foods. These are the two whitefishes and the two suckers. The round whitefish in Great Slave Lake eats mostly caddis larvae (43 per cent), gastropods (35 per cent) and chironomid larvae (21 per cent). The common whitefish does not compete greatly with the round whitefish, since its diet is made up mainly of amphipods (60 per cent) and sphaeriids (19 per cent). The suckers have a more mixed diet. The longnose species resembles the common whitefish in its food selection and, since it inhabits fairly deep water, it provides some competition for that species. The white sucker eats fewer amphipods and more chironomid larvae and, since it is restricted to the shallow water, its feeding is more like that of the non-commercial, round whitefish. However, the round whitefish is abundant only in cold water along rocky shores, while the white sucker is restricted to warmer water and usually to muddy shores. Thus they compete but little in any specific area. The only other species taking mostly bottom food is the grayling, which in Great Slave Lake took mostly amphipods

(43 per cent) and caddis (18 per cent). The grayling is a shallow-water species which takes a large variety of terrestrial insect food in addition to the bottom organisms listed.

The remaining species of fish include five piscivores, the inconnu, lake trout, pike, pike-perch and burbot. While the adults of these species usually eat fish, their young subsist on plankton and bottom fauna. Thus the stomachs of young inconnu were observed by Fuller (unpub., 1947) to contain chironomid larvae (25 per cent) and other insects (5 per cent). Even in the adult stage, piscivorous fish may feed heavily on bottom foods. Thus the lake trout took significant quantities of amphipods and caddis. The pike and burbot fed on amphipods and the pike-perch had taken 8 per cent of mayflies. The number of specimens of the goldeye from Great Slave Lake was too small to justify calculation of percentage volumes of food. However, it is known to take considerable quantities of insects, amphipods and gastropods in the restricted part of the lake which it inhabits.

TABLE VII. Approximate percentage by volume of bottom foods taken by the 12 large species of fish in Great Slave Lake.

	Amphipoda	Sphaeriidae	Gastropoda	Chironomid larvae	Trichoptera	Ephemeroptera	Other Aq. Insects	Ostracods	Oligochaetes	All bottom organisms
Goldeye *Amphiodon alosoides*	+		+			+	+			+
Round whitefish *Prosopium cylindraceum*		+	35	21	43		+			99
Common whitefish *Coregonus clupeaformis*	60	19	10	4	+	+	+	+	+	93
Ciscoes *Leucichthys spp.*	+			4	7		+	+		11
Inconnu *Stenodus leucichthys*	+			+	+					+
Grayling *Thymallus signifer*	43			2	18	+	+			63
Lake trout *Cristivomer namaycush*	4			+	3	+	+			7
White sucker *Catostomus commersoni*	30	9	11	32	17				+	99
Longnose sucker *Catostomus catostomus*	63	9	+	15	9	+	+			96
Pike *Esox lucius*	3				+	+				3
Burbot *Lota lota maculosa*	5	+			+					5
Yellow pikeperch *Stizostedion vitreum*	+					8	+			8

The ciscoes, probably representing three species, are the only adult plankton feeders in the lake. Even these take some bottom foods including chironomid larvae (4 per cent) and caddis larvae (7 per cent) (Rawson, 1951a).

Widespread sampling of the fish population has indicated that the common whitefish makes up 28 per cent of the total weight of the catch, lake trout 45 per cent, ciscoes 7.3 per cent, pike 3.8 per cent and the remaining species still smaller percentages. If these figures are taken as an indication of the actual composition of the population of the larger fish in Great Slave Lake, we may combine this information with that presented in Table VII to calculate that the bottom fauna of Great Slave Lake provides roughly 39 per cent of the food of fish (other than minnows and young fish) in the lake.

COMPARISON WITH THE BOTTOM FAUNA OF OTHER LAKES

Great Slave Lake may be considered as a member of a series of large lakes which continues northwest from the head of the Great Lakes, mostly along the margin of the Canadian Shield. This series includes Lake Winnipeg, Reindeer, Athabaska, Great Slave and Great Bear. Previous papers have shown considerable resemblance between several of these lakes in their physical conditions (Rawson, 1950) and in their fish populations (Rawson, 1951a). It is not surprising therefore to find a marked similarity in the bottom fauna of this series of lakes. In general they may be described as large oligotrophic lakes with bottom faunas dominated by the amphipod *Pontoporeia* and characterized by lesser quantities of sphaeriids *(Pisidium)*, oligochaete worms and chironomid larvae.

To facilitate comparison of the composition of the bottom populations in the large lakes of North America, Table VIII has been prepared by drawing together, from sources acknowledged in the table, data on the percentage numerical composition of the bottom fauna in eight lakes. In addition to six clearly oligotrophic lakes, two others, Simcoe and Waskesiu, are included to show the contrasting situation in a large mesotrophic and a moderately eutrophic lake. Lake Mendota could have been included as an example of a highly eutrophic lake, but this was not done because the quantitative data provided by Juday (1922) refer only to the deeper water of the lake.

The most striking feature of Table VIII is the dominance and relative constancy (61-72 per cent) of *Pontoporeia* in the first five lakes. Miller (1947) reports that *Pontoporeia* is the most abundant bottom organism in Great Bear Lake. A similar situation is known to exist also in Lake Superior (Eddy, 1943), although numerical data are not available. In Lake Nipigon fewer *Pontoporeia* and more chironomid larvae are found, while in Simcoe and Waskesiu there are relatively few amphipods and a heavy population of chironomids. It should be noted that *Pontoporeia* occurs in the first six lakes but not in Simcoe or Waskesiu. *Gammarus* and *Hyalella* are found in all of the eight lakes but, although locally abundant, they never contribute any large percentage to the total bottom population. *Pontoporeia* dominates the bottom fauna of all the very large lakes of northwest Canada and the Great Lakes except Lake Erie. The latter is warmer and relatively shallow. In it *Gammarus fasciatus* is the dominant amphipod, and *Pontoporeia* is found in relatively small numbers in the deeper water of the

TABLE VIII. Approximate percentage numerical compositions of the bottom fauna in eight large lakes in North America. (The authority for each lake is shown in parentheses.)

	Great Slave	Athabaska (Rawson, 1947a)	Reindeer (Rawson, unpub.)	Winnipeg (Bajkov, 1930)	Michigan (Eggleton, 1947)	Nipigon (Adamstone, 1924)	Simcoe (Rawson, 1930)	Waskesiu (Rawson, unpub.)
Amphipoda (mostly *Pontoporeia*)	62	61	72	64	64	34	4	4
Sphaeriidae (mostly *Pisidium*)	11	9	16	9	5	14	9	1
Oligochaeta	10	13	5	—	19	9	8	5
Chironomid larvae	8	11	4	0.4	—	37	61	66
Other aquatic insects	1	—	—	15	—	—	9	20
Gastropoda	3	2	1	1	—	5	5	1
Miscellaneous	5	4	2	—	10	—	4	3

eastern part of the lake (H. Clemens, personal communication). In considering *Pontoporeia* as the characteristic bottom organism of these deep lakes, reference should be made to the detailed study of the life history and ecology of this species in Athabaska and Great Slave Lakes by Larkin (1948).

Sphaeriids and oligochaetes are usually the second and third groups in the bottom fauna of our large lakes, though not always in the same order. Sphaeriids are still common in mesotrophic Lake Simcoe but are less frequent in more eutrophic lakes such as Waskesiu and Mendota. The larvae of certain species of chironomids form a small but fairly constant fraction of the bottom fauna of the deep lakes, and in one of them, Lake Nipigon, they constitute more than one-third of the bottom organisms. However, in Simcoe and Waskesiu Lakes the chironomids become dominant, as shown by values of 61 and 66 per cent. It should be added that *Chaoborus (Corethra)* also is important in Waskesiu, making up 19 of the 20 per cent listed in Table VIII as "other aquatic insects." In Lake Mendota, *Chaoborus* forms 75 per cent of the bottom fauna of the deeper water.

Lake Winnipeg, although much shallower than others of the oligotrophic series, has the same high percentage of *Pontoporeia* in its bottom population. It differs, however, in having an unusually heavy population of burrowing mayfly nymphs *(Hexagenia)* which make up most of the 15 per cent listed as other aquatic insects (Bajkov, 1930). In most of our lakes mayfly nymphs are abundant only in the upper 10 metres, and Lake Winnipeg is sufficiently shallow that they inhabit a large proportion of its area.

The average weight of bottom organisms per unit area in various lakes provides a means of comparison which supplements the numerical composition discussed above. Data for gravimetric comparison of the bottom fauna have been assembled in Table IX. Some of the lakes listed in Table VIII have not been included in IX because no gravimetric measurements were available, as in Lake Michigan, or because data were available only for certain areas of the lake, as in Lake Winnipeg. A value for Lake Ontario is included, but it should be noted that this is based on a single series of dredgings taken by Adamstone (1924). Some readers may note that the average of 24.7 kg./ha. for Waskesiu Lake is higher than that quoted in an earlier paper by the writer. The present value is based on a much larger number of dredgings (440) than the preliminary figure. The average dry weights of bottom organisms for the six lakes investigated by the writer are based on many dredgings (115 to 600) in each lake. The live or wet weights of organisms from each dredging were determined to the nearest milligram, and the equivalent dry weights were calculated using an average factor determined for the organisms in each lake. The average dry weight was found to vary from 12 to 20 per cent of the wet weight in different lakes. The average dry weight was calculated for each depth zone and the final average, presented in Table IX, is weighted according to the relative areas of the depth zones.

The average dry weight of bottom organisms in Great Slave Lake is recorded as 2.5 kg./ha. In Table V it was shown that the weight of organisms in the

separate areas of Great Slave Lake varied from 0.7 kg./ha. in McLeod Bay to 7.8 in Yellowknife Bay. All of these values are within the oligotrophic range, and that for McLeod Bay may be the lowest yet recorded for freshwater lakes. Lake Simcoe with 12.4 kg./ha. and Waskesiu with 24.7 are included in Table IX as examples of mesotrophic and moderately eutrophic types, respectively. Inclusion of Lake Mendota with 50.8 kg./ha. (Juday, 1922) would have provided a strongly eutrophic example but, as indicated above, the only available data are for the deep-water region and are thus not strictly comparable. Lundbeck (1926) provides data on the bottom fauna of 57 north German lakes averaging 1.1 km. in area and about 4.8 m. in mean depth. These lakes are in a eutrophic region although not all the individual lakes are eutrophic. The average dry weight of bottom fauna, exclusive of molluscs, in these lakes was 56.5 kg./ha.

In an earlier paper (Rawson, 1930) the writer compared the quantity of bottom organisms of Lake Simcoe, Ontario, with the data then available for other lakes and described what appeared to be a decrease in bottom fauna corresponding to both increase in area and increase in depth of these lakes. The problem was taken up by Deevey (1941) during his analysis of the bottom fauna of lakes in Connecticut. Assembling data from 116 lakes in North America and Europe, he was unable to find any mathematical expression for a relation between mean depth and standing crop of bottom fauna. He concluded that benthic productivity is influenced by many and complex factors and that it does not necessarily reflect the trophic type of a lake. However, in his 33 small and relatively shallow lakes of Connecticut he found a slight positive correlation of bottom fauna with mean depth. This he interpreted as probably due to the favourable nutritive effect on the bottom fauna of increased plankton production in greater depths of water (a thicker trophogenic zone). This positive correlation between bottom fauna and mean depth in shallow lakes is of special interest, in view of the apparent negative correlation between these parameters in large, deep lakes suggested below.

The long-term commercial fish production from the Great Lakes and several large lakes in Western Canada has been used by the writer (Rawson, 1952) as evidence of their productivity. Sustained fish production per unit area was found to correlate inversely with mean depth in a way described by the formula $p = \frac{30.255}{d^{0.7028}} + 0.5$ where p is sustained yield of fish in pounds per acre and d is mean depth in feet. This suggests that, in this group of lakes, morphometric factors are dominant in determining productivity (Rawson, 1952). A similar treatment of data for the standing crops of net plankton in lakes of Western Canada also demonstrated an inverse relationship with mean depth, described roughly by the formula $p = \frac{3765.0}{d^{1.5337}} + 8.0$ where p is the average dry weight of summer net plankton in kg. per ha. and d is mean depth in metres (Rawson, 1953). In both these relationships it was noted that the divergence of certain lakes could be attributed logically to differences in their climatic or edaphic

situations. To determine whether morphometric influences were also affecting the bottom fauna in our large lakes, the data for mean depth and weight of bottom organisms, from Table IX, were plotted in Figure 11. Since McLeod Bay is cut off from Great Slave Lake and Christie Bay shows distinctive features, the data for these regions are plotted in Figure 11 as well as the single figure which represents the average for the whole lake.

TABLE IX. Areas, mean depths and average weight of bottom organisms for several large lakes in North America.

	Area	Mean depth	Average dry weight of bottom organisms (mollusc shell deducted)
	sq. km.	*metres*	*kg./ha.*
Waskesiu	70	11.1	24.7
Simcoe	725	17.0	12.4
Athabaska	7,900	26.0	4.1
Minnewanka	13	38.1	4.5
Nipigon[a]	4,850	59.0	5.2
Okanagan	370	69.5	2.0
Ontario[a]	19,500	81.0	4.8
Great Slave	25,400	62	2.5
McLeod Bay	1,590	120	0.7
Christie Bay[b]	1,510	199	1.7

[a]From Adamstone, 1924.
[b]And adjacent bays.

The lakes represented in Figure 11 are all the large American lakes for which the writer has suitable data. There would be little point in including small lakes, since Deevey (1941) has demonstrated that they show no orderly relation

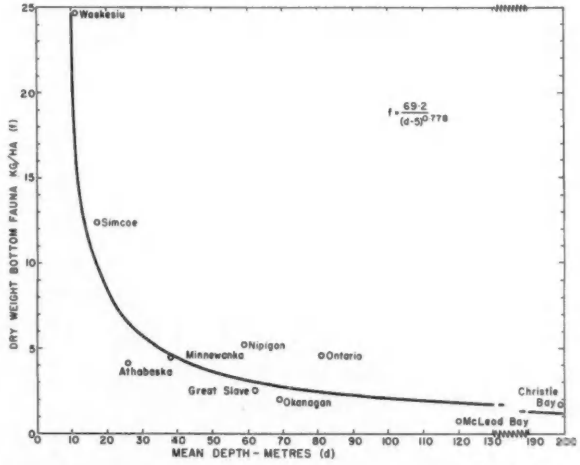

FIGURE 11. The relation between mean depth and average dry weight of bottom organisms in ten large lakes.

between mean depth and bottom population. Most of the lakes in Figure 11 are distinctly oligotrophic. Simcoe and Waskesiu are within the eutrophic range of mean depth, but from their plankton and oxygen relations it is clear that they are somewhat mesotrophic. Lake Mendota (area 39.4 km², mean depth 12.1 m. and deep water bottom fauna 50.8 kg./ha.) might have been included as a typical eutrophic lake, but our primary interest is in the large oligotrophic type.

The main observation from Figure 11 is that the group of deep oligotrophic lakes have standing crops of bottom organisms usually between 2 and 5 kg. dry weight per ha. (1.8-4.5 lb./ac.). In the extremely deep bays, Christie and McLeod, the population falls to 1.17 and 0.72 kg./ha., respectively. That McLeod Bay, though shallower than Christie, should have the lower bottom population is not surprising, in view of the evidence of unfavourable edaphic situation presented in a previous paper (Rawson, 195lb; McLeod Bay has only 22 p.p.m. total solids and Christie has 110). The value of 4.8 kg./ha. for Lake Ontario is tentative, since it is based on a single series of dredgings across the west end of the lake (Adamstone, 1924). An attempt was made to translate the numerical data of Eggleton (1937) for the bottom fauna of Lake Michigan to a gravimetric form. Using dry weights which had been determined for similar organisms in Great Slave and Lake Nipigon a crude value of the order of 5 kg./ha. was obtained for the open-water area of Lake Michigan. This resembles the value for Lake Ontario and is considerably greater than the average for other deep lakes listed in Figure 11.

Since climatic and edaphic factors are known to affect productivity and since mean depth cannot provide a complete index to morphometric influences, only a partial correlation should be expected. The data in Table IX have been subjected to a statistical analysis and the relation between mean depth (d) in metres and the bottom fauna (f) in kg./ha. is described by the equation,

$$f = \frac{69.2}{(d-5)^{0.788}}, \text{ or } \log f = 1.8401 - 0.778 \log(d-5).$$

This is the formula for the curve which is plotted in Figure 11. The visual impression of a reasonably good fit is supported by the high value of the index of determination, $p^2 = 0.783$. Nevertheless, the work of Deevey (1941) and others show that this should not be interpreted as a widely established relationship between mean depth and standing crop of bottom fauna. It can be expected to apply only to deep lakes and even in these a wide range of variation should be expected.

SUMMARY AND CONCLUSIONS

1. The bottom fauna of Great Slave Lake (area 27,000 sq. km.; 10,500 sq. mi.) was studied in the years 1944-1947 as part of a limnological and fisheries investigation. An account is given of the techniques used in taking some 600 dredgings and the data resulting from this study.

2. About 95 species of macroscopic bottom organisms have been identified from the collections. These have been listed with comments on their distribution.

3. The bottom population of Great Slave Lake is dominated by the amphipod *Pontoporeia affinis* which makes up 62 percent of the numbers of organisms. Other common organisms are sphaeriids *(Pisidium)* 11 per cent, oligochaetes 10 per cent, chironomid larvae 8 per cent, ostracods 3.5 per cent, gastropods 2.9 per cent and nematodes 1.5 per cent (Table I).

4. The inshore region (0-10 metres depth) has the heaviest bottom population. From 15 to 60 metres the average is about 1,600 organisms and 25.5 gm. per sq. metre. From this the population declines to about 300 organisms and 0.3 g. per sq. m. at 200 metres, and these amounts continue with little change to the greatest depth of 600 metres. Amphipods, oligochaetes, chironomids and ostracods are present at all depths. Gastropods are limited to the upper 40 metres. Sphaeriids are abundant near shore, but decline rapidly with depth and are absent below 300 metres. Nematodes are infrequent in the upper 50 metres, but increase to a maximum in the deep water (Table II, Figures 5 and 6).

5. Regional differences in the density of bottom population are indicated in Tables IV and V and Figures 7 and 8. Yellowknife Bay has one-third greater numbers and weight than the main lake. The population in the Islands area and in Christie Bay is somewhat lower than that of the main lake. McLeod Bay has less than one-third the number and only one-sixth the weight of organisms found in the main lake. The average dry weight of organisms is 1.7 kg. per ha. in Christie Bay and only 0.72 kg. per ha. in McLeod Bay.

6. The sparse bottom population of the great depths, 200-600 metres (Figure 9) includes single species of amphipod, ostracod, nematode, oligochaete, sphaeriid and chironomid. This is a remarkable contrast to the species swarms found in the depths of ancient lakes such as Baikal and Tanganyika.

7. The region of heavy silting and muddy water off the Slave River delta supports a bottom population more numerous and heavier than that of similar depths elsewhere in the main lake. In this muddy area, oligochaetes are 4.5 times and nematodes 3.5 times as numerous as are these groups in the remainder of the lake. The numbers of sphaeriids and ostracods are much reduced and gastropods appear to be absent from the delta region.

8. Bottom organisms provide about 39 per cent of the food of fish (not considering the food of minnows and young fish) in Great Slave Lake Table VII). Two species of whitefish and two species of suckers get more than 90 per cent of their food from the bottom fauna. About 63 per cent of the food of the grayling is made up of bottom organisms.

9. The bottom population of Great Slave Lake resembles that of Lakes Athabaska, Reindeer, Winnipeg and Michigan. In all of these, *Pontoporeia* is dominant and *Pisidium* and oligochaetes are common (Table VIII). Chironomid larvae appear in moderate numbers in these highly oligotrophic lakes and frequently dominate the fauna of eutrophic lakes. The average dry weight of bottom organisms in very large, deep lakes appears to range from 2 to 5 kg. dry weight per ha. Large eutrophic lakes have 5 to 10 times this quantity.

10. The average weight of bottom organisms in large oligotrophic and

mesotrophic lakes of Western Canada show an inverse relation to mean depth (Table IX and Figure 11). This is interpreted as indicating that morphometric factors are dominant in determining the productivity of these lakes.

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Preparation and Viscosity of Chitosans

By C. V. Lusena and R. C. Rose
National Research Laboratories, Ottawa[1]

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Other investigators have studied extensively the chemical properties of chitin and chitosan, but very little attention has been given to their preparation and properties as macromolecules. A study has been made, therefore, of the stability of chitin in solution and of the preparation and viscosity of chitosan.

Crude chitin was prepared from ground lobster carapaces by demineralizing with hydrochloric acid at pH not lower than 3 and extracting lipids with ethanol. Chitin has been considered stable in acid because it can be recovered from solution in concentrated strong acid (2, 3). However, viscosity measurements of this chitin in 45 per cent nitric acid and in 30 per cent hydrochloric acid showed that extensive degradation occurs even at 0°C., indicating that macromolecular studies of chitin in acid would be of little value.

In contrast to chitin, chitosans are soluble and quite stable in mild solvents. At least 65 per cent deacetylation was required to give a chitosan soluble in 0.1 M sodium acetate buffer (pH 4.6), which was the most suitable solvent for intrinsic viscosity measurements. This degree of deacetylation was obtained by treating one part of chitin with 100 parts of 55 per cent (w/w) potassium hydroxide solution for half an hour at 100°C. Decreasing the alkali concentration increased the time required to obtain soluble chitosans and the product was less viscous. Increasing the alkali concentration to saturation had little effect on deacetylation and viscosity. The size of chitin particle within the ranges 20-40 mesh, 40-60 mesh and 60-80 mesh had no effect on deacetylation and viscosity.

The size of chitosan molecules was most affected by demineralization treatment of lobster shells to obtain the crude chitin (see Table, page 522). Preparations demineralized at 5°C. without allowing the acidity to exceed pH 3.0 yielded chitosans of intrinsic viscosity 21, while preparations demineralized at room temperature and then left overnight in 5 per cent hydrochloric acid gave chitosans of intrinsic viscosity 4. Deacetylation in an atmosphere of nitrogen yielded chitosans of higher viscosity than deacetylation in air. Increasing temperature or time increased percentage deacetylation and reduced molecular size. One hour deacetylation in two half-hour stages separated by washing and air drying was as effective as one continuous 15-hour deacetylation and the product was more viscous. Even the most drastic deacetylation conditions used did not affect some 20 per cent of the acetyl groups.

A few ultracentrifuge and osmotic pressure measurements indicated extreme heterogeneity of the chitosans and the presence of large molecules or aggregates.

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This was confirmed by fractionation of lyophilized chitosan preparations with alcohol. Extraction of three chitosan preparations with 65 per cent ethanol raised the relative viscosity of 0.1 per cent solutions from 4.2, 13.8 and 38.2 to 6.0, 17.0 and 47.1, respectively.

It is concluded that chitin is attacked more easily by acid than previously reported. The instrinsic viscosity of some chitosans preparations is higher than that of most other naturally occurring polymers. A study of the relation of intrinsic viscosity to molecular weight of chitosan fractions could lead to a better understanding of the behaviour of very large long chain molecules.

DEACETYLATION OF CHITIN AND VISCOSITY OF CHITOSAN
(55 per cent potassium hydroxide used throughout)

Deacetylation conditions			Deacetylation[1]	Intrinsic viscosity of chitosan[2]
Atmosphere	Temp.	Time		
	°C	*hr.*	%	
Air[3]	100	0.5	68.0	15.4
Nitrogen[3]	100	0.5	65.0	21.5
Air	100	0.5	66.4	10.3
Nitrogen	100	0.5	68.5	12.4
Nitrogen[4]	100	0.5	66.9	4.0
Nitrogen	100	0.5	68.5	12.4
Nitrogen	110	0.5	72.7	11.6
Nitrogen	120	0.5	74.4	10.9
Nitrogen	130	0.5	76.9	9.7
Nitrogen	140	0.5	77.4	7.6
Nitrogen	100	0.5	68.5	12.4
Nitrogen	100	1.0	71.2	11.2
Nitrogen	100	3.0	76.4	10.2
Nitrogen	100	6.0	78.8	9.8
Nitrogen	100	15.0	81.2	7.9
Nitrogen	100	1.0[5]	81.0	10.6

[1]Measured by direct titration of free amino groups. Nitrogen determinations indicated that no deamination had occurred. (Clark's N-acetyl determination (1) was unsatisfactory for chitosans.)
[2]At 25° C. in 0.1 M sodium acetate buffer (pH 4.6) using A.S.T.M. Standard Fenske-modified Ostwald Viscometers.
[3]Chitin demineralized at 5° C.—all other samples demineralized at room temperature.
[4]After demineralization this preparation was left overnight in 5% hydrochloric acid.
[5]A portion of the 0.5-hr. deacetylated sample was air-dried and deacetylated for an additional 0.5 hr.

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Responses of Coho and Chum Salmon Fry to Current[1]

By Dixon MacKinnon and William S. Hoar
University of British Columbia and Pacific Biological Station

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ABSTRACT

Chum and coho salmon fry respond positively to changes in water flow by swimming against the current. The magnitude of the response varies with the intensity of the current. Currents eliciting optimum response differ for the two species. Both species respond to the stronger of two parallel laminar currents but, after a time, coho fail to discriminate between small differences while the chums move continuously into the greater flow. No evidence of adaptation is apparent in a two-hour period with rapid complex turbulences. In turbulent water coho fry make a sharper initial response than chum fry but do not seem to maintain the peak response over as wide a range of turbulences.

INTRODUCTION

Pacific salmon, dwelling in the turbulent streams on the mountainous west coast of North America, must react to currents which change drastically from day to day and from place to place. A difference has been observed in the character of response which coho fry (*Oncorhynchus kisutch*) and chum fry (*O. keta*) make to currents. This difference seems to explain, in part, why the former species remains in the rivers while the latter moves into the sea (Hoar, 1951). Responses of coho and chum salmon fry to current have not, however, been compared quantitatively nor has the character of the response been described in detail. Such an analysis is attempted in the present investigation.

The term *current* is used in this study to describe any motion of fluid within a body of water. When water moves in parallel layers or sheets the flow is described as *laminar*, whereas complex irregular movement or eddies within the liquid constitutes *turbulence*. It is unlikely that any of the experiments described here produced a strictly laminar flow. However, this condition was approximated in two groups of experiments where flow patterns are in marked contrast to the turbulent conditions developed in the third series.

MATERIALS AND METHODS

The current-preference experiments were conducted at Nile Creek, British Columbia, during the spring and summer of 1950.[2] The other experiments were performed at Port John, British Columbia, in 1951 and 1952. Chum salmon fry ranged in length from 25 to 45 mm., while coho fry varied from 40 to 65 mm. At Nile Creek, chum fry were retained in a wooden hatchery trough while

[1]Financial assistance was received from the National Research Council of Canada.

[2]These data are taken from a thesis presented by Dixon MacKinnon for the M.A. degree in Zoology at the University of British Columbia.

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the coho fry were kept in a holding box in the stream until three days before they were needed for experiments. They were then brought from the stream to the hatchery trough. At Port John, chum fry were sometimes used as captured but, more frequently, taken from a stock of fish held outdoors in a trough of running water. Coho were used as captured in the nearby stream.

At Nile Creek water temperature ranged from 9°C. in June to 16°C. in August. At Port John the range was 11° to 17°C. in 1951 and 9° to 18°C. in 1952. Constant temperatures could not be maintained, but the variations in holding troughs, in apparatus and in the nearby stream were essentially the same.

Laminar Flow Experiments

A. CURRENT PREFERENCE

The apparatus (Figure 1) was an enlarged modification of a trough designed by Shepard (1948) for salinity-preference experiments on chum salmon. It consists of a wooden trough with two reservoirs at the inlet end. Each of the two reservoirs leads by way of a ramp into an experimental chamber which is partially divided longitudinally. A screen placed across the trough a short distance from the end of the longitudinal partition divides the trough into an experimental and non-experimental chamber. A line on the floor of the trough from the point of the partition to the mid-point of the screen divides the common chamber in two. Water overflows the reservoirs into the divided portions of the trough. This provides two parallel flows which meet in the undivided portion of the trough and continue through the screen to the outlet. The width of this outlet is controlled by two adjustable glass plates. The experimental section of the trough is heavily coated with paraffin to prevent abrasion to the fish.

Water was drawn from the hatchery water system through rubber tubing to the reservoirs. To avoid disturbance, three sets of inflows were arranged so that the rate of flow into the reservoirs could be altered from a point beyond the visual range of the fish.[3]

The chum salmon experiments were performed outside the laboratory but within an area bounded by the white wall of the hatchery building on one side and white canvas tarpaulin on the others. Observations were made through a window or platform, well above the trough. Coho experiments were carried out in the laboratory under artificial light. These experiments, however, were checked qualitively by outdoor experiments and the reactions under study proved to be similar.

The method of studying responses to different flows was to present the fish with the alternative of moving into either of two different experimental flows. This method provides a well-marked motor response to demonstrate the discriminatory perception of the fish. Controls provided identical flows in both arms of the trough, while experiments (testing for reactions to flow differences) provided the control flow in one arm and an increased flow in the other.

[3]In the first series of chum experiments (Figure 4), a single inflow to each reservoir was used, and consequently fish were disturbed somewhat when flows were altered.

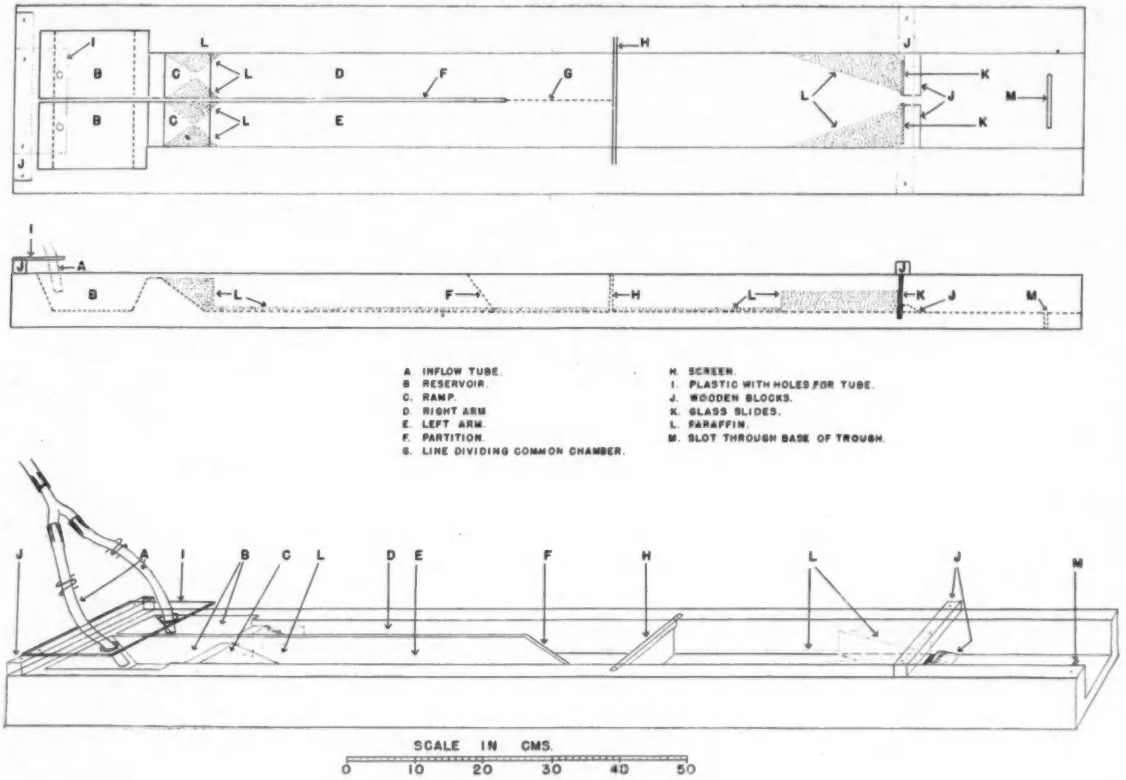

FIGURE 1. Current-preference trough.

Before each set of experiments, the water was turned on, flows were adjusted to the desired rates and the trough was allowed to fill (depth of about 4 cm.). When the trough was filled, 12 fish were placed in the undivided portion of the experimental chamber and retained there by a temporary partition for 20 minutes before the temporary partition was removed. The experiments began 10 minutes later. Each experiment lasted 16 minutes, during which time the number of fish on each side of the trough was recorded at one-minute intervals. The temperature of the water in each side of the trough was then recorded and the inflows were changed for the next experiment. One hour later observations were repeated. Between experiments, water flow continued and fish were free to roam in the different areas of the trough. From four to eight experiments were performed on a new lot of fish each day. To avoid bias, inflows were alternated between the right and left arm.

B. UPSTREAM MOVEMENT THROUGH SHALLOW WATER

Shallow water flowing down a slope was used to stimulate upstream movement. Comparisons were made in a trough 360 cm. long, 30 cm. wide, and 20 cm. deep. Within the trough, three areas of equal length (120 cm.) were recognized—the upstream pool, the ramp or rapids and the downstream pool. The rapids (central) area contained a plywood ramp sloping from a height of 15 cm. at its upper end to the floor of the trough at its lower end. The trough was slightly inclined so that water (8,000 to 9,000 ml./min.) entering the upper end of the upstream pool flowed over the ramp to create shallow water on the upper 15 to 20 cm. of the ramp. The overflow pipe at the lower end of the downstream pool was 15 cm. high. To pass from the lower to the upper pool the salmon swam through water so shallow that their backs were exposed. A 45-cm. length of black paper over the ends of the trough provided the possibility of cover at the ends of the pools. The interior of the trough was painted black.

In these experiments, 10 chum and 10 coho salmon fry, previously held for at least one hour in quiet water, were placed together in the downstream pool, watched for 15 minutes and the number passing into the upstream pool noted. In addition, a record was made of all fish which swam far enough into the shallow water to expose their backs (unsuccessful attempts). At the end of two hours a final record was made of the distribution of the fry.

Turbulent-Flow Experiments

The stimulus in these experiments was turbulent water issuing from large glass tubes. The apparatus was assembled in galvanized iron troughs painted with aluminum engine enamel. The troughs were 240 cm. long, 25 cm. wide and 10 cm. deep. A removable screen 15 cm. from one end separated an area containing an adjustable overflow pipe from the main portion of the trough and thus limited the working length of the trough to 225 cm.

In one group of experiments, two 65-mm.-diameter glass tubes 600 mm. long, were arranged side by side, about 70 mm. apart, in the trough with the inflow ends of the tubes 500 mm. from the end of the trough. This end of the tube was

fitted with a rubber stopper which was pierced by a 100-mm. length of glass tubing 13 mm. in diameter. These smaller glass tubes passed through a plywood partition at this point in the trough and could be readily connected to the water tap by 13-mm.-diameter rubber tubing. The depth of water in this trough was maintained at 80 mm. Water was drawn from a 1,500-gallon (6,825 litres) storage tank. The tank was filled in the morning and evening and the temperature varied somewhat less than the temperature of the creek water in which the stocks of fish were maintained. Long periods of rainy weather provided almost constant temperature and light conditions. It was impossible to maintain constant temperatures, but the variations occurring in the experiments were of the same order as those in the stream water where the fish lived.

Water flowed into only one of the two tubes during any particular experiment. This tube is referred to as the "current tube" while the other, receiving no water, is the "quiet tube". The two tubes were used alternately as the "current tube" in duplicate experiments, and flows were standardized by measuring the amount of water flowing through the system in millilitres per minute. These values were related to the flow conditions in the trough by injecting dye into the water flowing through the tubes (Figure 2). Whenever a series of different flows was used, the order for the series was determined by random numbers. A complex pattern of turbulent currents created in and around the tubes stimulated rheotactic responses in the fish. Similar apparatus was assembled in paired troughs using 50-mm.-diameter tubes (Figure 3) and water

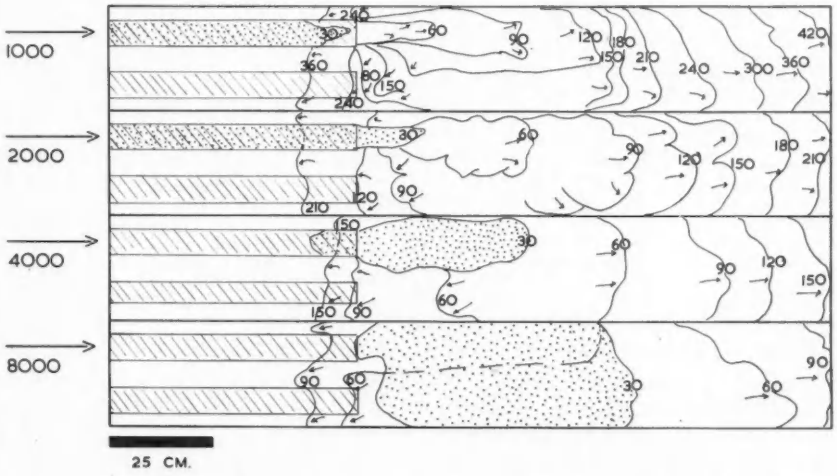

FIGURE 2. Four diagrams showing patterns of currents in trough when four different volumes of water (ml./min.) are forced into 65-mm. glass tubes. Cross-hatched areas, glass tubes; arrows at left with numbers, flow in ml./min.; stippled area, distribution of 5 ml. saturated methylene blue 30 sec. after rapid injection into inflow tube; irregular curved lines and small arrows show position of dye front at intervals in seconds as indicated by numbers on lines; further description in text.

130 mm. deep in the trough. The smaller tubes resulted in relatively faster flows and the deeper water gave more complex turbulences. With the smaller tubes results were less consistent but of the same order.

Observations on groups of 20 to 25 fish were made for 15-minute periods, five times per day. In general, experiments were set up about 11:00 A.M. each day and observations made at 2:00, 4:00 and 7:00 P.M., and at 7:00 and 10:00 on the next morning. Water was suddenly turned on to the desired rate of flow and remained constant for the 15-minute observation period. It was turned off between observation periods when the fish were permitted to roam about the apparatus. Positions of the fish were recorded, at 30 second intervals for 15 minutes, with respect to the two tubes, the area around the tubes and the area downstream from the tubes. In an attempt to prevent conditioning, the same groups of fish were observed for only two days. New groups of fish were seined from the retaining pens and those used on the previous day then returned to the pens.

The apparatus is not ideal. Turbulences used as stimuli are complex and vary qualitatively at the different rates of flow. In addition, fish can see through the glass walls and a small amount of nipping and schooling was sometimes noted between the individuals inside and outside the tubes. Numerous observations were necessary to smooth out the resulting inconsistencies. Finally, it was necessary to guard against gradients in the dissolved gases, since the water was sometimes turned off for as long as three hours before stimulating the fish. Dissolved oxygen was checked frequently by the standard Winkler method for all groups of fish and various flow conditions. No gradient in dissolved

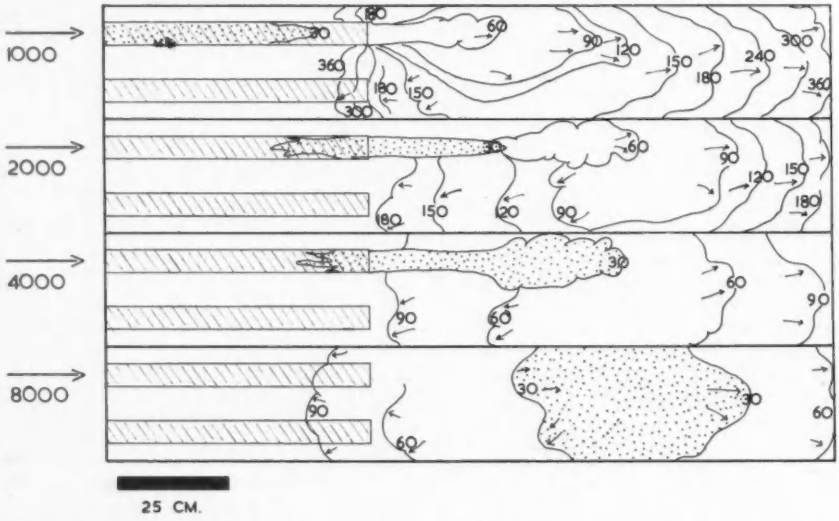

FIGURE 3. Pattern of currents and arrangement of 50-mm. tubes used to study responses to turbulence. See legend Figure 2 and text for description.

oxygen was found under any experimental conditions. This is no doubt owing to the activity of the fry and the fact that they do not rest in the quiet tubes. Values obtained varied from 8.8 to 9.2 mg. oxygen per litre over a temperature range of 12° to 16°C.

RESULTS

Flow Preference

The flows used in these tests were of relatively low velocity and approximately laminar in character. They probably provided the most constant type of current used in this study. Fish moved freely to and fro in this apparatus and experienced no apparent difficulty or intense stimulation with respect to the currents.

CHUM FRY

A series of experiments in which the inflow to one arm was equal to (four experiments), double (six experiments), triple (four experiments) and quadruple (four experiments), that of the other arm shows that chums move into the area that is influenced by the greater inflow. The strongest response occurred when the flow into one arm was triple the flow into the other (Figure 4).

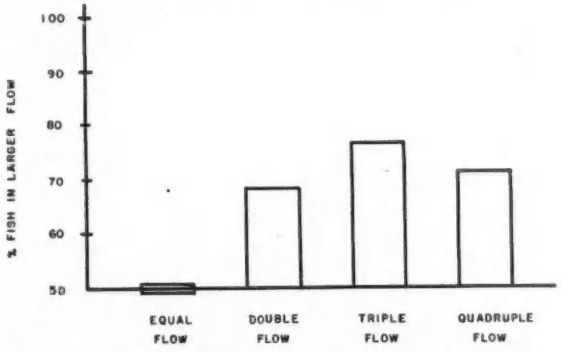

Figure 4. Responses of chum fry to differences in flow velocity.

In the next series (eight experiments with each flow condition), one arm of the trough received an inflow of 200 ml./min. and the other arm received inflows of 200, 350, 500, 600 and 700 ml./min. Again there is a decided preference for the area having a greater flow (Figure 5). In this series the greatest response toward the faster flow occurred when the variable arm of the trough received an inflow of 500 ml./min., i.e. a flow difference of 300 ml./min.

In the above experiments the water temperature in the arm having the faster flow was equal to or from 0.1 to 0.6 Centigrade degrees lower than the temperature of the other arm. The difference was brought about by the warming of the water flowing through the tubes. The next series (four experiments with each flow condition) was designed to determine if similar responses occurred when the water temperature in the arm having the increased flow was higher

than that of the lesser flow arm. Hot water was added drop-wise to the reservoir with the faster flow. The results (Figure 5) show that the reaction was not greatly changed by an increased temperature in the faster flow when the temperature in the double inflow side of the trough (400 ml./min.) is 0.5 Centigrade degrees higher than that of the other inflow (200 ml./min.), or when the water in the quadruple inflow side (800 ml./min.) has a temperature 1.3 Centigrade degrees higher than that of the other inflow side (200 ml./min.). These temperature differences are greater than those encountered in the previous experiments, in which the temperature was greater in the lesser flow.

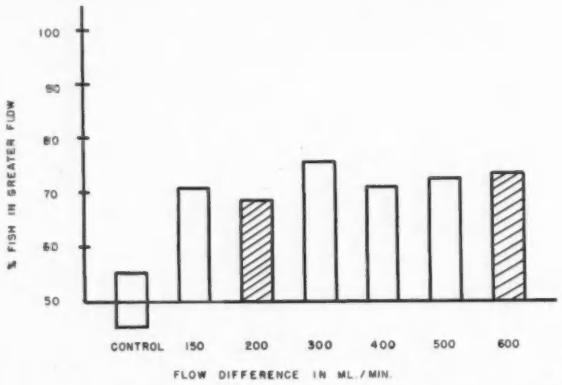

FIGURE 5. Responses of chum fry to differences in flow velocity. Open bar, temperature in greater flow equal to or from 0.1°-0.6°C. lower than that of lesser flow; cross-hatched bar, temperature in greater flow is higher (0.3°-0.5°C. at 200 ml./min.; 1.0°-1.3°C. at 600 ml./min.) than that in lesser flow.

In Table I the means for numbers of fish in the two channels of the trough have been compared statistically. The probability values of .01 show that the chum response is uniformly toward the greater flow.

A series of qualitative observations carried out at night indicates that the chum response to the greater flow persists after dark.

TABLE I. Comparison of responses of chum and coho salmon fry to differences in water flow. In each case water in channel B moved at the greater rate. Each observation period consisted of 16 one-minute intervals.

	Chum					Coho					
	Flow difference in ml./min.					Flow difference in ml./min.					
	0	150	300	400	500	0	100	200	300	400	500
Number of observation periods	8	8	8	8	8	6	4	4	4	4	4
Mean number of fish per period of 16 minutes	A 5.1	3.5	2.6	3.1	3.3	5.8	5.8	5.3	5.5	5.6	5.1
	B 6.2	6.8	9.0	6.2	8.8	6.4	5.7	6.7	6.9	6.4	6.4
Pooled t	2.20	4.63	7.94	3.43	12.14	0.96	0.09	1.22	2.72	0.48	1.00
Pooled P	0.05<0.01		<0.01	<0.01	<0.01	0.33	0.90	0.24	0.04	0.65	0.31

COHO FRY

Coho fry were studied in seven different flow conditions. One arm always received 200 ml./min. while the other was varied from 200 ml./min. to 800 ml./min. at intervals of 100 ml./min. Six control (equal flow) experiments and four experiments with each flow difference were performed. The experiments were carried out in an underground laboratory where the air temperature was nearly equal to the water temperature, consequently there was no differential warming of water in the two arms of the trough. Artificial light provided equal illumination over all areas of the trough.

The results (Figure 6) indicate that the coho fry do select the greater of two flows but the response is not as great as that of the chums (Figure 5). The statistical analysis (Table I) shows that the difference between mean numbers of coho in the two channels is not significant.

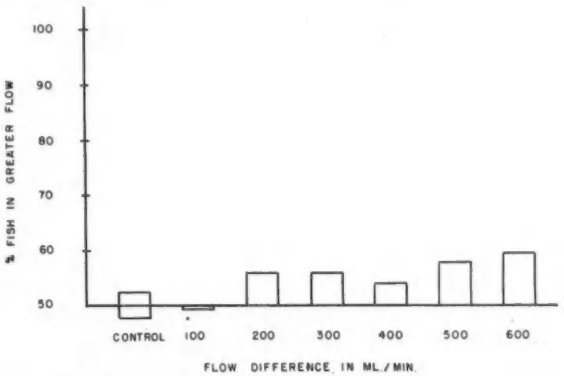

FIGURE 6. Responses of coho fry to differences in flow velocity.

In Table II responses of coho fry are compared during the first three and last three hours of exposure to current. The initial response to greater flow changes to an indifference and in some cases a preference for the lesser flow during the daily period of study.

TABLE II. Changes in response of coho fry with time.

Flow ratio in two arms	Ratio of response into two arms	
	1 to 3 hours	4 to 6 hours
200: 300	198: 187	192: 192
200: 400	132: 252	208: 176
200: 500	198: 222	162: 222
200: 600	178: 205	176: 209
200: 700	122: 263	207: 177
200: 800	102: 282	231: 185
Totals	926: 1411	1176: 1161
Chi-square	99.8	0.1

Night observations on coho show that they, like the chums, respond to faster flows—at least initially—after dark.

Adaptation to Current

These comparisons of chum and coho fry in the two-channel current-preference trough show an interesting variation in rates of adaptation of the two species. This is most conclusively demonstrated in the statistical analysis of Tables II and III.

Coho fry become indifferent to laminar currents of relatively low intensity during a period of two hours, while chum fry show a steady response at all flow differences.

Table III. Changes in response of chum fry with time.

Flow ratio in two arms	Ratio of response into two arms	
	1 to 3 hours	4 to 6 hours
200: 200	162: 222	160: 176
200: 350	123: 261	99: 295
200: 500	60: 305	86: 298
200: 600	101: 187	75: 307
200: 700	101: 283	110: 274
Totals	550: 1258	530: 1350
Chi-square	138.5	178.8

Upstream Movement through Shallow Water

In these experiments, water flowing from an upstream to a downstream pool over a ramp stimulated fish to move up through the shallow water over the ramp. Young salmon placed in the downstream pool show a characteristic reaction pattern. They immediately dart under the cover, but within five minutes or less are swimming back and forth as a group between the edge of the cover and the central area of the ramp. With each excursion individuals come closer to the somewhat turbulent area at the bottom of the shallow water on the ramp until some enter this and dart rapidly through the shallows to the upstream pool. Frequently fish are swept back before they attain the upper pool. In these experiments, fish were never observed to move from the upper to the lower pool.

Quantitative data for six groups of fish involving 18 periods of observation are presented in Table IV. It is evident that chum fry are more persistent and more successful in swimming through the shallow water. The ratio of attempts to successes is lower for chums, and almost twice as many chums attained the upper pool in the first 15 minutes. Again, it is apparent that although all of the chum fry (10) may swim into the upper pool during the first 15 minutes, coho never showed the maximum response during this period. This experiment

Table IV. Mean numbers of fish moving from a downstream to an upstream pool through shallow water. Ranges given in brackets; maximum successes, 10.

	Chum	Coho
Attempts—15 min.	4.9 (0–13)	3.2 (0–7)
Successes—15 min.	3.5 (0–10)	1.8 (0–4)
Successes—2 hr.	6.3 (1–10)	4.0 (0–10)
Attempts/successes—15 min.	1.4	1.8

confirms other data showing that chum salmon fry respond more vigorously than coho fry to current.

Turbulent-Flow Experiments

When water was not flowing through the apparatus, most of the 20 to 25 salmon fry used in these experiments were seen to swim about in the lower

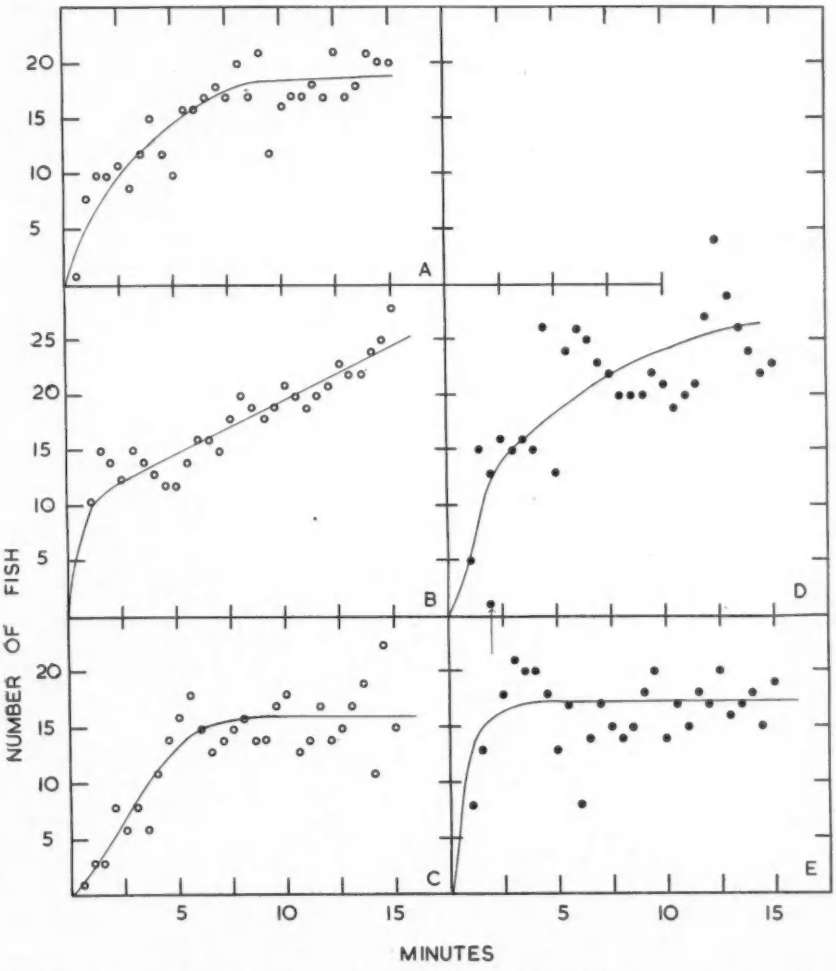

Figure 7. Responses of salmon fry to turbulence. A, coho fry, 900 to 1,200 ml./min., 15.5°-17.5°C.; B, coho fry, 6,000 to 7,000 ml./min., 13.0°-16.0°C.; C, coho fry; 10,000 to 14,000 ml./min., 14.0°-17.0°C.; D, chum fry, 6,000 to 9,000 ml./min., 14.0°-17.0°C.; E, chum fry, 12,000 to 14,000 ml./min., 16.0°-17.0°C.; time in minutes after flow started; number of fish, total fish entering current tubes in three separate periods of observation; trend lines fitted by eye; further description in text.

end of the trough, while few occupied the areas in and around the glass tubes. In the case of chum fry, the large glass tubes may have interfered with their schooling activities. In the case of coho, the areas in and around the tubes were occupied and defended by a few individuals against the majority which remained downstream.

When the current is started in one tube, the fish immediately show a change in activity and within a few seconds swim up towards the tubes. Individuals occasionally enter the "quiet tube", often swim into the areas around the tubes, but most frequently move into the "current tube". However, the response is never complete in the sense that all fish enter the "current tube". Moreover, the distribution is continually changing with the to-and-fro movements of the fish. If all 20 fish remained in the current tube for the 15-minute period (observations at 30 seconds) the recorded response would be 600. The greatest response ever recorded was 327. The greatest number recorded in the "quiet tube" for a comparable period was 13 fish. Simple observation indicates clearly that the fish are stimulated by the current to swim into the "current tube", and the number of fish recorded there seems to be a reasonably good measure of their response.

The response to turbulence is shown in relation to time in Figure 7. These data were obtained with groups of 25 fish in the 65-mm.-tube apparatus. Data

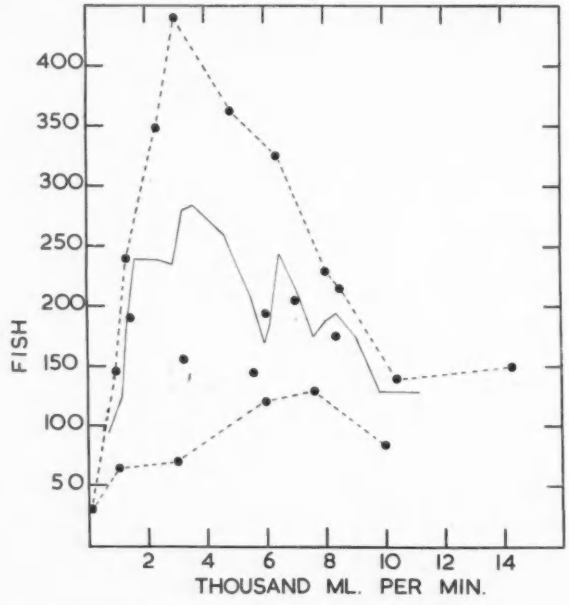

FIGURE 8. Response of coho fry to sudden change in current; solid circles, total response for 15-minute period of observation; continuous line is drawn by joining points obtained from moving averages of two taken twice; broken lines, upper and lower limits of response; further description in text.

from three different observation periods have been totalled for each of the flow conditions indicated. It is evident that the response rises more or less rapidly to a peak value varying with the turbulence. At intermediate flows (Figure 7, B, D), both chum and coho fry show a more gradual attainment of maximum response. In the less turbulent waters (Figure 7A) and in the strongest turbulences (Figure 7C, E), the response rises to a maximum within 5-7 minutes. At intermediate flows the peak does not seem to have been attained in the 15-minute period of observation. The character of the response of these fish to turbulence shows general features of stimulus-response mechanism (Heilbrunn, 1952), in that the rate of rise to peak value varies with the intensity of stimulation.

These data suggest that there may be an optimum current for maximum response. In figures 8 and 9 data obtained the same way are presented for a larger series of turbulences. In this case total number of fish moving into current tube minus number moving into the quiet tube is plotted against the turbulence used. The coho data (Figure 8) are less regular than the chum data (Figure 9), but in each case there is evidence of a maximum response at intermediate turbulences. The coho value is evidently attained at lower intensities of stimulation and reaches a higher value than the chum response. On the other hand, the maximum chum response may be more prolonged. It is not possible to establish such a difference for the two species, however, since the coho and chum fry at this season are in different physiological conditions (Hoar and Bell, 1950).

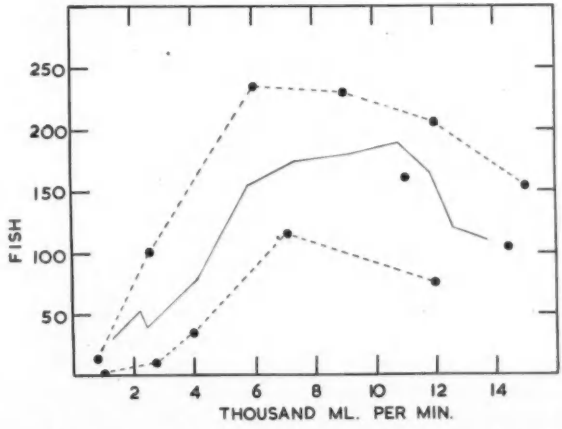

FIGURE 9. Response of chum fry to sudden change in current. See legend for Figure 8 and text.

Coho fry were also observed in the 50-mm.-tube apparatus. In this case, groups of 25 fry were studied, but otherwise the experimental procedure was the same. In Figure 10 the responses of coho fry exposed to sudden turbulence are compared to fry which were exposed for at least two hours to the particular

turbulence before positions were recorded. The nature of the response is almost identical and again shows a maximum in each case at about 4,000 ml. per minute. A less complete series of experiments carried out with chum fry in this same apparatus showed a maximum at 8,000 ml./minute and again the curve had a flat top with prolonged response from about 5,000 to 8,000 ml./minute. These data confirm those obtained with the 65-ml. tubes. No convincing evidence of adaptation was obtained with these complex turbulences. In fact, the response shows higher maximum values when the fish are exposed to the turbulence for a longer period.

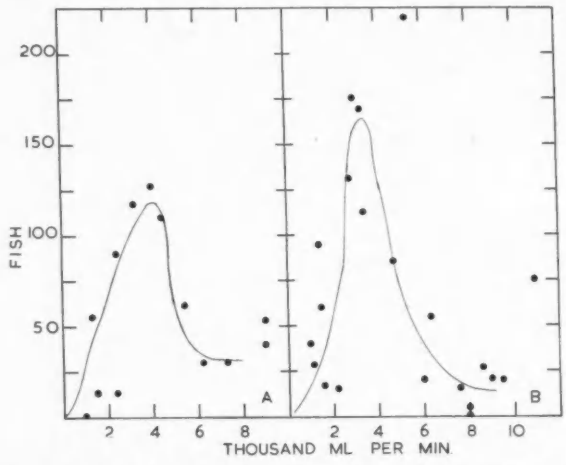

FIGURE 10. Response of coho to turbulence. A, total response during 15 minutes when current rises suddenly from zero to peak values; B, total response during 15 minutes following a two-hour period of exposure; trend lines drawn through points obtained from moving averages of two taken twice.

DISCUSSION

Both coho and chum salmon fry show a strong positive rheotaxis. This simple description, however, gives little information concerning the effects of water currents on the distribution of salmon fry. Such behaviour may lead to any one of three effects. The fish may maintain their position in the current, they may be gradually displaced downstream or they may be stimulated to migrate upstream. All three effects have been observed, at least over short distances, with coho and chum salmon fry. Careful analysis of the response in relation to known turbulences and current is necessary before accurate predictions can be made. Responses to current are dependent upon the stimulation of recognized sense organs and the character and nature of the response should be studied and analysed in reference to well-established characteristics of the stimulus-response mechanism (Heilbrunn, 1952). Of particular importance in an analysis of the

behaviour of fish in current will be measurements of the strength of stimulation giving maximum response, and a comparison of rates of adaptation or accommodation. In this connection, the present study has revealed several features which may be pertinent to an understanding of the behaviour of coho and chum salmon fry.

The sharp, almost immediate, positive response displayed by both species in strong turbulence will counteract downstream displacement, at least during the day. The persistent optimum response, shown at certain intensities of stimulation (Figures 8-10), may be the basis of upstream movements sometimes observed. The fact that chums apparently discriminate more sharply and consistently between currents of different intensity, and uniformly move into the more rapid flow, should take them into faster water than the coho.

Neither species showed adaptation to very turbulent waters. Both showed a prolonged response which at certain intensities (Figure 7, B, D and Figure 10) became progressively more marked over a two-hour period. Elson (1939) found that trout (*Salvelinus fontinalis*) previously acclimatized for three days to quiet water, showed a marked response to current for a period of about two hours, after which they evidently showed adaptation. In the present experiments, fish were never exposed to quiet water for more than two hours before experimentation. When Elson's fish were held in still water for only two hours prior to experimentation, the response lasted only 10 minutes. The experimental conditions were entirely different, but the data indicate that duration and strength of response may depend on the previous history of the fish. Some of the irregularity in comparative results may be due to the variable history of the fish prior to experimentation.

Turbulences obtained with the glass-tube apparatus may not be satisfactory for demonstrating differences in rates of adaptation in the two species. These turbulences are very complex, although probably no more complex than those frequently encountered in natural habitats. Laminar flows of the selection trough (Figure 1) are simpler, and it may be assumed that the type of stimulation will be more uniform over a long period. In this case, marked adaptation was evident in coho but not in chum. After a prolonged period the coho fry failed to make a definite response to the greater flow. The possible significance of this adaptation has been mentioned.

It would be impossible to explain the migratory behaviour of juvenile coho and chum salmon on the basis of their response to current alone. In both cases, the movement will be into the current and sometimes upstream. The sharp response made by both species to sudden change in turbulence will prevent their downstream displacement—at least during the day. The chum, showing a strong response over a wider range of turbulences and failing to adapt to small differences in flow, will be more likely to move into fast waters where downstream displacement is likely at night. Other behaviour patterns must, however, be of more significance in explaining the difference in migratory behaviour of these salmon. In particular the strong preference which chum show for light (Hoar, MacKinnon and Redlich, 1952) will keep them up from the bottom and take

them into the open and relatively swift parts of the stream during the day. At night the marked activity of chums in contrast to nocturnal settling behaviour of coho is important in explaining their downstream displacement after darkness (Hoar, 1951).

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Experiments with the Harbour Seal, Phoca vitulina, a Definitive Host of a Marine Nematode, Porrocaecum decipiens[1]

By D. M. Scott
Atlantic Biological Station[2]

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ABSTRACT

Infestation experiments carried out in 1947 and 1948 showed that the harbour seal (*Phoca vitulina*) was a definitive host of a larval nematode found in the flesh of the Atlantic cod (*Gadus callarias*), smelt (*Osmerus mordax*), Canadian plaice (*Hippoglossoides platessoides*) and eelpout (*Macrozoarces americanus*). Adult worms recovered from experimentally infested seals were identified as *Porrocaecum decipiens*. Some larval *Porrocaecum* in the four species of fishes studied were *P. decipiens*.

The worms lost their larval characteristics by moulting between the third and sixth day following introduction into the seal. Sexual maturation proceeded rapidly after the eleventh day and some males and females matured before the twentieth day. Maturation was accompanied by a distinct increase in size.

INTRODUCTION

The Atlantic cod, *Gadus callarias* Linnaeus, and several other marine fishes in inshore Canadian waters are commonly infested with a parasitic nematode. This parasite is most commonly located in the musculature of the host. Although it is improbable that the worm is harmful to man (Martin, 1920; Kahl, 1938), the distraction awaiting a sensitive consumer can be easily imagined. Consequently, the widespread occurrence of this worm presents a grave problem not only to the fresh-fish industry but also to the canned-fish industry in the Atlantic provinces of Canada. Fish processors frequently employ workers whose sole function is the removal of worms from fillets, a procedure which is obviously expensive.

A study was begun in 1945 on the life history of the parasite in an attempt to disclose some stage vulnerable to human control. The problem was studied by Mr. Friedel Schiffman until his death in 1946 and continued by the author until 1950.

All the worms examined from cod muscle were larvae. Most of them indisputably belonged to the genus *Porrocaecum* Railliet and Henry of the sub-

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[2]Author's present address: Department of Zoology, University of Western Ontario, London, Canada.

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family Anisakinae (Yorke and Maplestone's classification, 1926). This genus of *Ascaris*-like worms is characterized by the presence of a digestive caecum which distinguishes it from a closely related genus *Anisakis* in which the caecum is absent (Bayliss, 1920). However, small specimens, presumably *Porrocaecum*, may lack this caecum and hence be generically indistinguishable from *Anisakis*. Not only do the larval characteristics of the cod-worm occasionally prevent proper generic identification, according to Bayliss (1944), but they also do not permit satisfactory specific identification. One of the major points of this investigation was the determination of the species involved.

Adult ascarids, *Porrocaecum decipiens* (Krabbe), have been reported from the stomachs of several species of seals (Stiles and Hassall, 1899; Baylis, 1916) and these authors believed that seals were definitive hosts for the larval worms in fish. They speculated that seals became infested by eating fish, that the parasites matured in the seal and that the eggs of the worms returned in faeces to the sea whence they returned directly or indirectly to fish, thereby completing the cycle. Since, however, no specific characters have been described for the larvae, this evidence suggesting that the worms in fish and the adult worms in seals belong to the same species is circumstantial and not conclusive.

The most conclusive proof of this proposed relationship might best be obtained by the experimental infestation of seals with *Porrocaecum* larvae from fish, followed by observations on the subsequent fate of the worms. This paper reports upon a series of experiments of the above type whose primary purpose was to discover whether or not the harbour seal, *Phoca vitulina* Linnaeus, was a definitive host of *Porrocaecum* larvae from cod. It was also hoped that the specific identity of *Porrocaecum* larvae in cod, smelt, *Osmerus mordax* (Mitchill), Canadian plaice, *Hippoglossoides platessoides* (Fabricius), and eelpout, *Macrozoarces americanus* (Bloch and Schneider), could be determined.

MATERIALS AND METHODS

Four harbour seals in 1947 and twelve in 1948, about one month old, were obtained from the U.S. Fish and Wildlife Service at Boothbay Harbour, Maine. These young seals had been captured in nets and, infrequently, in this process some seals were drowned. The stomach of a drowned seal contained milk only, showing that at the time of capture at least some of the seals were still unweaned and that seals of this age were probably free from worms. While in captivity at Boothbay Harbour, the seals were offered herring, *Clupea harengus* Linnaeus, but there was no information to indicate that the herring were eaten by all the seals. As far as is known, no other fishes were given to the seals.

The seals, upon their arrival at St. Andrews, were separated into pairs and kept in pens which were approximately 8 ft. x 4 ft. x 2½ ft. A platform upon which the seals could rest was built at one end of each pen. In 1947 the pens were filled with sea water which entered at one end of the enclosure and passed through the four pens. The flow of water seemed unsatisfactory, so in the following year new pens were built and set in a tidal pool where the water was renewed and circulated by normal tidal action. Even this method,

although adequate, was not entirely satisfactory, for the sides and floors of the pens soon became thickly covered with algal growth which was difficult to remove. The seals refused food for the first two or three weeks of their captivity at St. Andrews, but at the end of that time they began to eat herring.

Herring were chosen as the most suitable food because they formed an important part of the diet of harbour seals in this area (Fisher, 1951), because they were readily available at St. Andrews and because they were not known to be infested in this area with *Porrocaecum*. Accordingly, herring were unlikely to be a source of *Porrocaecum* for the seals. The herring were, however, infested with a species of *Anisakis*. Approximately three pounds of fresh or frozen herring were fed daily to each seal. In 1947, with only four seals to feed, it was possible to use fresh herring most of the time, but in 1948 the food requirements of twelve seals were so great that it was necessary to use frozen herring to a greater extent than in 1947. When most of the seals would accept food from my hand and swallow it at once, the seals were placed singly into individual pens and the experiments were started.

The experimental plan consisted of the introduction into certain seals of a known number of worms removed from the muscles of cod, smelt, plaice or eelpout. It was assumed on the basis of their previous feeding history that the seals were free of *Porrocaecum* worms at the beginning of the experiments. Only large worms, 25 to 50 mm. long, presumably with the generic characters of *Porrocaecum* already developed, were used. They were placed in the mouths of fresh herring which were then fed to the seals. If the fish were not swallowed immediately, they were recovered and discarded. Fresh fish containing more worms were then offered to the seals. This procedure was followed until the fish were swallowed immediately, and thus it was possible to be reasonably certain of the number of worms swallowed by a seal. Other seals were fed only herring without artificially introduced worms, and these seals acted as the control animals for the experiments. In 1947, three seals were used as test animals while the fourth served as control. Eight test animals and four controls were used in 1948. Apart from the worms fed to the test animals, the diets of the two group of seals were essentially the same.

The collection of the worms requires some explanation. Whenever possible, worms newly removed from fish caught near St. Andrews were used. However, worms from cod were not easily obtained at St. Andrews in the quantity needed for the experiments, and it was occasionally necessary to have large numbers of worms shipped to St. Andrews. I am indebted to Mr. D. N. Fitzgerald for the collection of worms from cod fillets at Lockeport, N.S., and Caraquet, N.B. The worms were shipped in jars of sea water and, upon arrival, dead worms were removed and the remainder were transferred to fresh sea water and kept at a temperature of approximately 14°C. The sea water was changed daily and, in this manner, the worms were maintained in an active condition for periods as long as four weeks. Thus, some of the cod-worms used in the experiments had been removed from cod several weeks before their introduction to the seals. Worms from other species of fishes were collected at St. Andrews and were

usually given to the test seals within a day or two of their removal from the fish.

The hypothesis which was to be examined assumed that the worms mature in the stomach of a seal and that the eggs of the worms pass out in the faeces of the seal. Consequently, before and after the introduction of worms into the test seals, faecal samples were collected as often as possible from all test and control animals and examined for nematode ova. Ten smears from each faecal sample were examined. The presence of ova in a smear indicated the existence of a mature female worm within the seal, and the time between the initial infection and the appearance of ova in the faeces was an indication of the time required for the sexual maturation of female worms.

Test seals were shot after sufficient time had elapsed to permit the maturation of some of the worms present in the seal. The digestive tract was removed and carefully examined. Any nematodes present were killed in hot 70 per cent alcohol and later transferred to fresh 70 per cent alcohol. The worms were cleared in lactophenol and mounted in glycerin jelly for examination.

Three stages of development were recognized: larval, immature and mature. Larval worms were characterized by the presence of a boring tooth of cuticular origin and a cuticle which entirely covered the incompletely developed lips. The immature and mature worms lacked the boring tooth and possessed three distinct lips which were individually covered by the cuticle. This sharp distinction between larval and post-larval stages made easy the recognition of the two stages. The presence of large eggs in the uteri of the females and well-developed testes and seminal vesicles in the males were criteria of sexual maturity. These criteria of maturity are admittedly arbitrary and it is possible that some of the worms judged as immature were really mature.

Mortality among the seals was high. In 1947, two test animals and one control animal died, apparently from an intestinal disorder. The symptoms and duration of the illness were similar in all three animals: the seals refused food, became lethargic and excreted bloody, liquid faeces and death occurred within 24 to 48 hours after the appearance of the symptoms. Post-mortem examinations showed extensive inflammation of the mucosa of the stomach and intestine. In 1948, a control animal stopped eating and died within a week; no abnormal conditions in the internal organs were noted. Later in 1948, after the author's departure from St. Andrews, one control and two test animals died. In each case, death was preceded by a period of at least a week during which the animal refused to feed. The cause of death was unknown.

RESULTS

The details and results of the experiments are summarized in Table I.

Faecal smears from the controls were always negative.

One nematode was recovered from the stomach of one control animal; no worms were found in the stomachs of the four other control seals. No worms were present in the oesophagus or intestine of these seals. The single worm recovered was a small (24 mm.) larval worm which lacked the intestinal caecum characteristic of many *Porrocaecum* larvae of this size. It probably belonged to

TABLE I. Details and results of seal experiments in 1947 and 1948. The day of the first introduction of worms into a test animal is indicated as D 0, subsequent days as D 1, D 2, etc. The times of deaths of the controls are given as the number of days after they began to eat herring.

Controls (C) Tests (T)	Date of introduction (D)	Number of worms	Source of worms	Death in days after start of experiment	Number of worms in stomach	Percentage return of worms introduced	Observations
1947							
C1		—		14*	0	—	—
T1	0	30	Cod				
	2	50	Cod	6*	65	61.9	Day 6: all worms larval or immature *Porrocaecum.*
	3	25	Cod				
T2	0	30	Cod				
	2	50	Cod	14*	76	72.4	Day 14: all immature *Porrocaecum;* sexual differentiation noted.
	3	25	Cod				
T3	0	20	Cod				
	3	20	Cod	24	11	20.8	Day 17: immature *Porrocaecum* recovered from regurgitated food; Day 20: ova in faeces; Day 24: 2 mature male *P. decipiens,* 2 mature and 7 immature female *Porrocaecum.*
	4	13	Cod				
1948							
C2		—		18*	0	—	—
C3		—		44	0	—	—
C4		—		52	1	—	Larval worm, *Anisakis* sp. (?).
C5		—		104*	0	—	—
T4	0	50	Cod	17	1	2.0	Day 17: immature female *Porrocaeum.*
T5	0	50	Cod	17	0	0	—
T6	0	50	Cod	18	6	7.5	Day 17: several ova in faeces; Day 18: 1 mature male *Porrocaecum decipiens,* 1 mature female and 4 larval *Porrocaecum.*
	15	30	Cod				
T7	0	50	Cod				Day 20: 1 mature female *Porrocaecum* recovered from regurgitated food. No ova observed in faeces.
	33	60	Cod	76*	0	0	
	34	85	Cod				
T8	0	50	Cod	89*	0	0	Day 10: 1 immature *Porrocaecum* recovered from regurgitated food. Day 19: no ova observed in faeces. Day 28: numerous ova in faeces.
	22	40	Cod				
T9	0	25	Smelt				Day 22: several ova in faeces. Day 25: 1 mature male *P. decipiens,* 1 mature and 3 immature female *Porrocaecum,* 1 immature *Porrocaecum,* 1 larval *Anisakis* or *Porrocaecum* sp.
	4	5	Smelt	25	7	14.3	
	10	19	Smelt				
T10	0	10	Plaice				Day 34: 4 mature male *P. decipiens.* No ova were observed in faeces during experiment.
	4	7	Plaice	34	4	5.0	
	16	23	Plaice				
T11	0	35	Eelpout	29	2	2.9	Day 29: 2 mature male *P. decipiens.* No ova were observed in faeces during experiment.
	4	35	Eelpout				

* Natural death

the genus *Anisakis* and was possibly introduced with the herring which were parasitized by a species of *Anisakis*.

Faecal smears from test animals prior to the introduction of worms were invariably negative. Ova were first noted on Day 17 (test animal 7) but in other animals did not appear until Day 20 or later.

Larval, immature and mature worms were recovered from the stomachs of five of the eight seals which had been fed worms from cod; no worms were found in the intestines. All the worms belonged to the genus *Porrocaecum*. At death, the three remaining test seals contained no worms. However, the presence of worms in two of these seals had been indicated during the experiments by a mature female *Porrocaecum* regurgitated by test animal 7 on Day 20 and by numerous ascarid ova in the faeces of test seal 8 on Day 28.

Test animals 9, 10 and 11 which had been fed worms from smelt, plaice and eelpout, respectively, contained worms in the stomach when killed. All the worms with one exception, a small larval *Porrocaecum* or *Anisakis*, belonged to the genus *Porrocaecum*.

The characters of the mature male worms were compared with the descriptions of *P. decipiens* (Baylis, 1916; Stiles and Hassall, 1899). They agreed in all essentials. It was concluded from their association with male *P. decipiens* that, although they lacked good specific characters, the mature female and immature *Porrocaecum* recovered from test seals belonged to this species.

DISCUSSION

The complete absence of worms belonging definitely to the genus *Porrocaecum* and the negative faecal smears from the controls throughout the experiments indicate (1) that the seals were free from worms upon their arrival at St. Andrews, and (2) that the herring, fed to control and test animals alike, did not introduce *Porrocaecum* worms into the seals. Thus, the presence of worms in the stomachs of test animals must have been the result of the experimental introduction of worms. It is concluded, therefore, that under experimental conditions the harbour seal was a definitive host of the larval *Porrocaecum* from cod. The identification of the adult worms showed that at least some of the worms in cod were larval *P. decipiens* as were also the larval *Porrocaecum* found in smelt, eelpout and Canadian plaice.

The numbers of worms recovered from the seals in the 1948 experiments were very small, much less than had been anticipated after the results of the 1947 experiments. The reasons for this difference are unknown. It cannot be attributed to age differences in the seals, for the animals in both years were all less than two months old when the experiments began. The diet in 1948 contained proportionately more frozen herring than in the previous year. It is possible that this type of food may have had an adverse effect upon larval worms, since there is some evidence to suggest that a heavy mortality occurred in the worms soon after their entrance into the seals. Test animal 6, originally fed with 50 cod-worms on Day 0, received an additional 30 worms on Day 15; yet when it was killed on Day 18 only four larvae, one mature male and one mature female

were found, thus indicating a high mortality between the juvenile and mature stages.

It has been suggested that the low returns in 1948 indicate that the harbour seal is not a natural host. This view is contradicted by the success of the 1947 experiments and by the fact that wild harbour seals, young and old alike, in east-coast waters frequently contain large numbers of *P. decipiens*. The author in 1948 observed *P. decipiens* in the stomachs of eight harbour seals captured in widely separated localities of the Maritime Provinces. Recently, more detailed studies by Fisher (1950, 1951) on more than 125 stomachs of harbour seals showed that *P. decipiens* was abundant in most harbour seals.

It was possible to learn a great deal about the development of the worms within the definitive host by the examination of worms recovered either from regurgitated food or from the stomachs of the seals. In several cases, the length of time the worms had been in the seals was known within a day or two and morphological differences permitted the recognition of various stages of development.

Larval worms after their entrance into a seal, moult, lose the characteristic larval boring tooth and enter the definitive stage. All worms recovered from test animal 2 were immature; these worms represented those that had been introduced into the seal 11, 12 or 14 days previously. Because the number recovered was about 25 per cent less than the original number introduced, it is impossible to state definitely that any worms had been in the seal for exactly 11 or 14 days. Undoubtedly, however, many worms had been in the seal for only 12 days and, therefore, the cuticular boring tooth of many worms must have been lost by the twelfth day. This was corroborated by the recovery of an immature worm from food regurgitated by test animal 8 on Day 10. Test animal 6 contained two mature and four larval worms on Day 18; as worms had been given to this animal on Days 0 and 15, the larvae were most likely part of those introduced on Day 15. The cuticles of three were thick, loose and partly withdrawn from the body of the worm. The entire appearance was that of a moult. From this evidence and that derived from the study of test animals 2 and 8, it is concluded that the change from larval to definitive form occurred between the third and twelfth day within the seal.

A moult was also observed in worms recovered from test animal 1 three to six days following their introduction. These worms were placed in a petri dish containing sea water and left overnight at a temperature of 18° to 22°C. The following morning the moulted cuticles of almost half the worms were found in the petri dish. The majority of the worms were immature with no visible sexual characters. Although this moult occurred under abnormal circumstances, it seems unlikely that it would have occurred unless the worms were already approaching a moulting condition. The evidence indicates, then, that the definitive stage was reached following a moult which occurred after the third day, and probably before the sixth day after the entrance of the larvae into a seal.

Sexual differentiation proceeded rapidly following the eleventh day. The sex of the immature worm recovered on Day 10 from test animal 8 could not be determined; however, worms recovered after 11 to 14 days in test animal 2 showed a wide range of sexual development. The sex of some could not be determined, but in many the reproductive organs were clearly developed although no worms were judged to be mature.

Females apparently took at least 16 days to reach an egg-laying condition. Nematode ova were first noted as early as Days 17, 20 and 22 in test animals 6, 3 and 9, respectively. Large mature females were recovered as early as Days 18 and 20 in test animals 6 and 7. On the other hand, in test animal 3 seven of nine females were judged to be immature, although they had been in the seal for at least 20 days. The period required for sexual maturation evidently varied greatly; at least 16 days but, in most cases, several more days were required so that for most females maturity was probably not reached until 20 days had elapsed.

The scanty data concerning males did not indicate any great difference between the sexes in the time needed for sexual maturation. A mature male was collected from test animal 6 on Day 18. Both male worms recovered after 20 to 24 days in test animal 3 were mature. In the latter case, fertilized ova were observed in faecal smears by Day 20 suggesting that by this time at least one male worm was mature. These times are similar to those required for the maturation of females.

The maturation of both sexes was accompanied by a great increase in size. Most larval worms used in the experiments were 30 to 40 mm. long with very few worms exceeding 50 mm. in length. Most female worms, immature or mature, recovered from seals were longer than 50 mm.; the longest was 78 mm. Males were also larger than the larvae, but were distinctly smaller than the mature females.

SUMMARY

Larval parasitic nematodes, *Porrocaecum* sp., from the flesh of four species of marine fishes, cod, smelt, Canadian plaice and eelpout, were fed to 11 young harbour seals, *Phoca vitulina*. Evidence of infestation was observed in 10 seals. All worms, with one exception, recovered from the test seals belonged to the genus *Porrocaecum*. The mature males were identified as *Porrocaecum decipiens*, and it was concluded that mature female and immature worms belonged to the same species. One worm, probably an *Anisakis* sp., was recovered from a control animal. Four other control animals showed no signs of infestation.

The experiments demonstrated that the harbour seal was a definitive host of larval *Porrocaecum* from four species of fish and that at least some of the *Porrocaecum* in cod, smelt, Canadian plaice and eelpout were larval forms of *Porrocaecum decipiens*.

The development of the worms within the seal has been discussed. A moult, in which the larval characters were lost, occurred at least three days after

entrance of the worms into a seal. The worms then entered an immature stage differing from the mature stage only in the extent of sexual differentiation. Sexual differentiation was not observed by the tenth day, but was well advanced by the fourteenth day. Nematode ova, noted in the faeces of a seal on the seventeenth day, indicated that a female worm had matured by that time. However, the majority of females required at least 20 days to reach maturity. Males developed sexually at about the same rate as the females. Maturation, particularly in the females, was accompanied by a marked increase in size.

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The advice and direction of Dr. T. W. M. Cameron, Director of the Institute of Parasitology, McGill University, and Dr. W. R. Martin, Atlantic Biological Station, St. Andrews, N.B., are gratefully acknowledged. The co-operation of the staff of the U. S. Fish and Wildlife Service, Boothbay Harbour, Maine, who captured and donated the seals used in this study, is warmly appreciated.

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Preliminary Experiments Using Lights and Bubbles to Deflect Migrating Young Spring Salmon

By J. R. Brett and D. MacKinnon
Pacific Biological Station, Nanaimo, B.C.

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ABSTRACT

Experiments to deflect young spring salmon during their night-time migration by means of a beam of light and/or a "wall" of bubbles were conducted in a canal near Courtenay, B.C. By use of hoop nets it was discovered that under natural conditions no significant difference existed in the respective catches of the spring salmon underyearlings moving downstream on either side of the canal. A significant difference was obtained, however, when a narrow beam of light was directed into the water at a downstream angle in front of one net. A reduction to about one-third the expected catch resulted with either continuous or flashing light. The "wall" of bubbles, in a similar position, did not reduce the catch.

Cut-throat trout fry and hatchery-reared Kamloops trout fingerlings were not deflected under these conditions.

INTRODUCTION

The problem of altering the downstream migratory path of young salmon, with a view to their safe passage around destructive barriers, is one of prime importance in fisheries conservation. At present no universally satisfactory means has been devised whereby the multitude of salmon fry and fingerlings moving downstream can be diverted from passing through turbines, over spillways or into large irrigation intakes. Rotating screens (Leitritz, 1952) have been used with success in small streams, but where log booms, ships and fish all use the same rivers, and where large volumes of water are concerned, no mechanical screening method has been considered feasible. The possibilities of using electrical "screening" have attracted more attention than any other approach to the problem (Hólmes, 1948) and although such a method has shown some promise (Groody *et al.*, 1952) there is still no technique in accepted use.

Since it is common practice among fishermen to thrash the water and pound on the sides of their boats in order to scare fish into a netted area, it seemed quite possible that by duplicating these factors in a more mechanical fashion young salmon might be deflected in their downstream movement. Turbulent water, flashing light and intermittent sounds stimulate visual and auditory receptors in the fish, and an avoiding response results. It was therefore proposed to set up a "wall" of air bubbles extending part way across a stream and to illuminate this area with continuous or flashing light. By testing these factors singly and in combination their usefulness could be ascertained.

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LOCATION AND METHOD

A concrete- and brick-lined canal, approximately 1,000 feet (305 m.) long, carries water from a diversion dam in the Puntledge River to a cement pipeline leading to the Canadian Collieries powerhouse, Courtenay, B.C. The canal is 26 feet (8 m.) wide and slopes from either edge in the form of a flattened "V" to a central depth of 7 feet (2.1 m.). The relatively constant flow and uniform contour of the canal suggested the possibility of an equal distribution of young spring salmon (*Oncorhynchus tshawytscha*) moving downstream on either side of the canal. By setting nets of identical size in each half of the canal the distribution could be recorded and the effects of the deflecting gear assessed through their influence in altering the catch in one of the two nets (Figure 1).

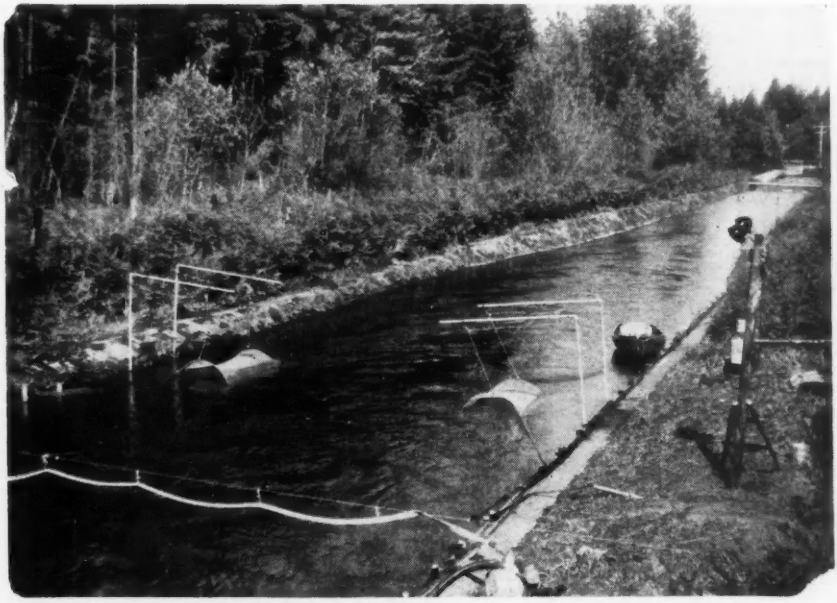

FIGURE 1. View showing the upstream end of the hoop nets suspended in the canal by rope and wire cable. Between the light pole and water pump (right foreground) a portion of the galvanized iron pipe and rubber hose for carrying exhaust gases is visible.

Large hoop nets were employed for this purpose. A cylindrical leading portion of the net, 4 feet (1.2 m.) in diameter and 6 feet (1.8 m.) long, was terminated by two bags, one slung within the other. The inner bag (3 feet long) and forward section of the net were hung with ½-inch (1.3 cm.) stretched, cotton mesh, while the outer bag (4 feet long) was hung with marquisette of fixed opening, 4/16 by 5/16 of an inch (.64 by .79 cm.). A rust-proof zipper in the side of the outer bag permitted ready access to the pursed inner bag. A side arm

of netting bridged the gap between the canal edge and the hoop net, five feet out. An area of approximately 12.6 sq. ft. (1.17 sq. m.) was provided by the opening of a single net. Together with the side arms, the two nets presented an upstream surface area of about ⅓ the total cross-sectional area of the canal. The nets were designed for operation in the fast current of the canal with a surface velocity of 3 feet (1 metre) per second. The large straining surface of the forward netting permitted rapid flow of water through the nets. The small fish either were caught by the larger mesh of the inner bag or wriggled through to be picked up by the finer, outer mesh.

To produce the "wall" of bubbles, 20 feet (6.1 m.) of ⅝-inch (1.6 cm.) copper tubing was drilled with holes 1/32 inch (.08 cm.) in diameter and ¼ inch (.64 cm.) apart. The perforated tube was placed in the bottom of the canal with one end in the centre and the other at the edge, making an angle of approximately 40°. Rubber hose connected the lower end of the tubing to the exhaust pipe of a truck. As the bubbles rose from the tubing those nearest the deepest point were swept farthest downstream before reaching the surface. The angle described by the surfacing bubbles and the canal edge approximated 25° (Figure 2).

Light was obtained from three sealed-beam headlights mounted on a pole about 20 feet (6.1 m.) from the bubble wall, and run from the truck generator.

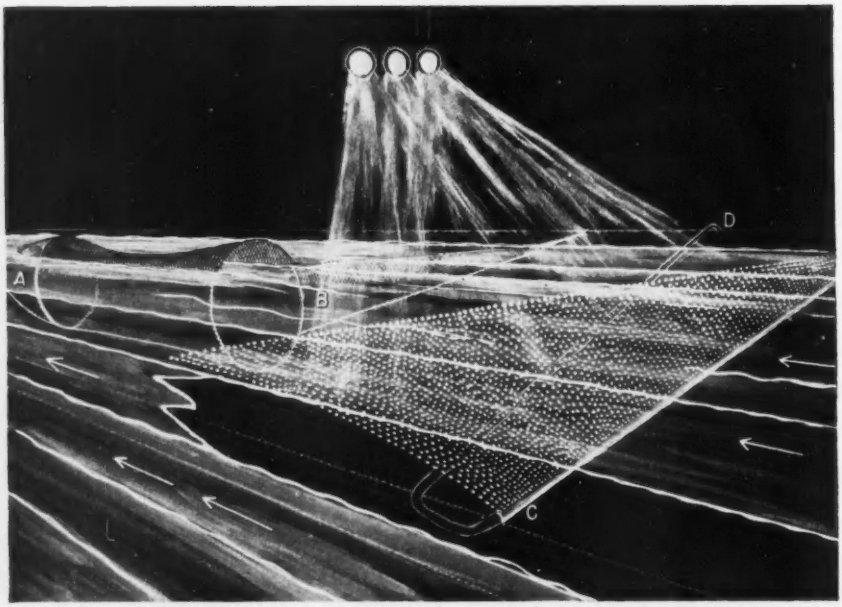

FIGURE 2. Semi-diagrammatic drawing of deflecting apparatus showing wall of bubbles rising in front of one net. A—double-meshed bag; B—side arm of netting; C—perforated copper tube; D—rubber hose carrying exhaust gases. (Drawn by D. Denbigh)

The lights were adjusted in position and masked in such a way that a narrow beam of light illuminated the bubbles. The incident light intensity at the water surface for a point of maximum illumination was 3.5 foot-candles. By connecting flashers in series with the headlights, continuous or flashing light (breaking once per second) was available. No illumination of the nets, set below this point, back from the light beam, could be measured at night using a light meter sensitive to 0.005 ft.-c.

Control and deflection tests were conducted during the period June 5 to June 29. Previous exploratory netting and direct observation of the fish established a characteristic night migration. Nets were set between the hours of 8:30 and 9:30 p.m., Pacific Standard Time, and lifted after three to four hours fishing when deflecting techniques were in use; when no deflection was being tested (control nights) the nets were usually left in the water for eight to nine hours and lifted in the morning. An effort was made to test each factor or combination of factors at least twice and to intersperse deflection nights with control nights, as the migration changed numerically and different weather conditions prevailed.

FISH PRESENT

The Puntledge River is one of the most productive salmon streams on the east coast of Vancouver Island. Spring (*O. tshawytscha*), coho (*O. kisutch*), chum (*O. keta*) and pink salmon (*O. gorbuscha*) spawn in some part of the river and its tributaries, the latter two mainly in the lower stretches. In addition, rainbow or steelhead trout (*Salmo gairdneri*) and cut-throat trout (*Salmo clarki*) are present in abundance. A portion of the progeny of spring salmon, steelhead and cut-throat trout pass into the canal from the upper reaches of the river, above the diversion dam. Cut-throat trout fry were caught in greatest abundance, averaging 32.72 $\pm$ 1.63 mm. in length and 0.27 g. in weight. The young spring salmon averaged 58.9 $\pm$ 3.0 mm. in length and 2.02 g. in weight, and showed a perceptible increase in size during the netting period. Only a few rainbow trout were caught, owing in part to their size (up to 250 mm.) which was apparent from anglers' catches. Sticklebacks (*Gasterosteus aculeatus*) and sculpins (*Cottus asper*) were also present in the net catches.

Kamloops trout (*Salmo gairdneri kamloops*) were obtained from the Puntledge River Park Hatchery for experimental releases into the canal above the nets. Their average live weight was approximately 5.0 g. (90 to the pound). The smaller of these trout were more readily caught and those taken averaged 71.8 $\pm$ 10.7 mm. in length and 3.7 g. in weight.

RESULTS

Spring Salmon

A total of 531 young spring salmon were caught during the 25 nights of netting. The daily catches are plotted in Figure 3. Some of the variation was undoubtedly due to the effects of the deflecting gear, and there was some indication that overcast or rainy nights resulted in higher catches than clear, cool

nights. The size of the fish tended to increase as the run proceeded. Since the catchability of the fish decreased with size, the observed drop in catch toward the end of the experiment cannot be completely ascribed to a reduction in migration.

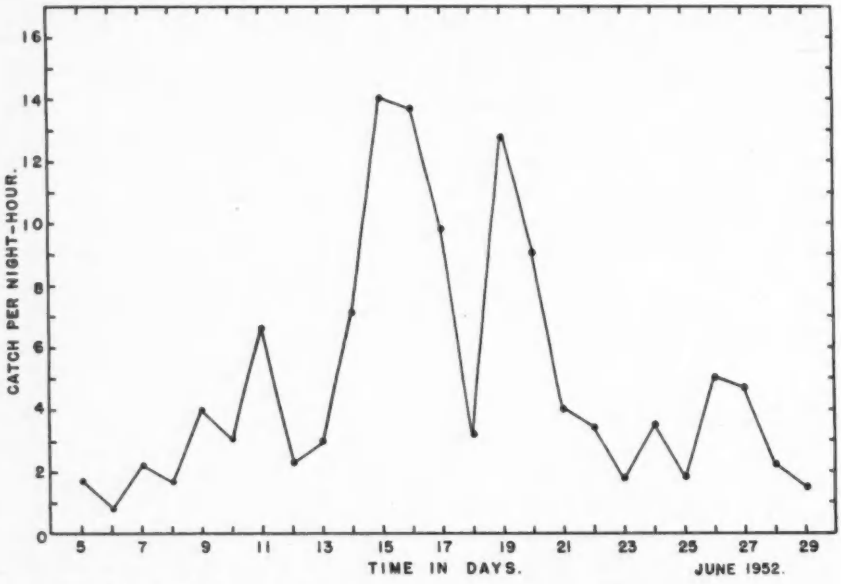

FIGURE 3. Number of young spring salmon caught in both nets per night-hour of fishing, on successive nights of June, 1952.

Nine nights were devoted to comparison of catches between the two nets with no deflection apparatus in operation. The premise for comparison between control and deflection results was based on the hypothesis of no significant difference between catches in the two nets during control nights. To test this hypothesis a chi-square test was used, comparing the actual catches with the best measure of the expected catch, i.e. the mean value (Table I). The P-value obtained was 0.99, indicating a high degree of similarity in catches. This is reflected in the total control catches of 60 and 59 for right and left nets, respectively. The high probability value of 0.99 is sufficient to suggest the presence of some influence causing a distribution more even than random.

With this basic assumption of equality of distribution demonstrated, the effects of the various deflecting factors can be assessed. The left net (facing upstream) was always the net subject to deflection effects. It would have been a more difficult undertaking to arrange for the transporting of the gear from one side of the canal to the other. The catches in the 11 "deflecting" nights are presented in Table II. Definite deflection was achieved. The most effective single agent was the beam of flashing light. It was apparent that any of the tests

involving light had a positive deflecting effect. The wall of bubbles used alone did not cause sufficient reduction to be considered of significance under these circumstances. The most effective single night of deflection occurred on June 26, an overcast night, using bubbles plus flashing light, when the fraction of catch in the left net was approximately one-sixth that of the right net. No significant difference was present in the *size* of the fish from deflected and non-deflected catches.

TABLE I. Catches of young spring salmon during control nights. Difference between catches has been tested for significance by chi-square, using the mean catch as the best measure for the expected catch.

Date	Catch			χ^2
	Right	Left	Mean	
June 5	5	5	7.5	0.06
6	3	2		
7	7	6	6.5	0.08
8	6	4	5	0.40
9	13	11	12	0.16
13	9	9	9	0.00
18	8	11	9.5	0.48
25	4	7	10	0.20
28	5	4		
Total	60	59		1.38
		d.f. = 7		P = 0.99

TABLE II. Total catches of young spring salmon during deflection nights. Difference tested by chi-square using the mean catch as a measure of the expected catch.

Factor	No. of nights	Catch			χ^2	P
		Right	Left	Mean		
Bubbles (B)	3	22	14	18	1.78	.19
Light, continuous (L–c)	2	28	9	18.5	9.76	$<.01$
Light, flashing (L–f)	2	75	20	47.5	31.8	$<.01$
(B) + (L–c)	2	35	11	23	12.6	$<.01$
(B) + (L–f)	2	19	7	13	5.6	.02

CUT-THROAT TROUT

The number of trout fry (Figure 4) caught in the two nets totalled 4,080. These fish were observed only along the very edge of the canal, up to one foot in depth. Their apparent inability to stem the current at greater depths made deflection around the nets unlikely. A significant difference in the catches between the two sides existed for control nights (Table III). The right net had a total catch of 1.14 times that of the left, so that the hypothesis found applicable to the spring salmon (equal distribution) did not apply in this case.

A consideration of the control and deflection results shows sufficient variation between the catches in left and right nets to preclude attaching any significance to the somewhat increased ratio of right to left net (1.69 to 1) during

deflection nights (Table IV). In particular the increased variability between catches observed during control tests towards the end of the experimental period (June 25 to 28, Table III) must be noted. All the deflection tests were conducted within the period June 11 to 30. While satisfactory deflection might

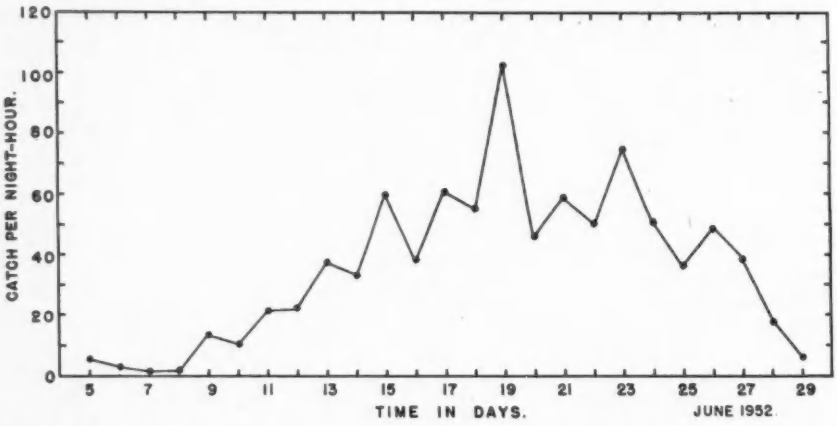

FIGURE 4. Number of cut-throat trout fry caught in both nets per night-hour of fishing, on successive nights of June, 1952.

TABLE III. Catches of cut-throat trout fry during control nights. Difference tested by chi-square

Date	Catch			χ^2	Ratio
	Right	Left	Mean		Right/Left
June 5	16	23	19.5	2.50	0.70
6	10	10	10	0.00	1.00
7	6	5			1.20
			11.5	4.26	
8	9	3			3.00
9	48	42	45	0.80	1.14
13	135	126	130.5	0.62	1.07
18	195	189	192	0.20	1.03
25	148	104	126	15.34	1.42
28	47	23	35	16.46	2.04
Total	594	523		40.18	Av. = 1.14
		d.f. = 8			$P < .01$

TABLE IV. Total catches of cut-throat trout fry during deflection nights.

Factor	No. of nights	Catch		Ratio
		Right	Left	Right/Left
Bubbles (B)	3	368	224	1.64
Light, continuous (L–c)	2	186	90	2.07
Light, flashing (L–f)	1	96	112	0.80
(B) + (L–c)	1	25	11	2.27
(B) + (L–f)	1	145	48	3.02
Total	8	820	485	Av. = 1.69

be achieved with lower stream velocities, under the conditions in the canal this did not appear possible.

Kamloops Trout

Three releases of hatchery-cultured trout, amounting to 2,000, 2,000 and 3,200, respectively, were made in the canal 300 yards (275 m.) above the point of deflection. These were intended to supplement the spring salmon returns by using a fish large enough to be capable of avoiding the deflecting apparatus in the rapid flow of water. Of the recaptured fish (259), no indication of significant difference in the catches was present for either control (ratio, right to left net = 1.12) or deflection periods (ratio = 1.25).

The time of release was shortly after 10:00 p.m. in each case. Floats liberated at the same point were swept down to the netting position within 2 minutes, 50 seconds. Although some trout were obtained within 20 minutes after release, the majority were not caught until 3 to 11 hours later despite the fact that by 9:00 p.m. photometer readings had dropped below 0.005 ft.-c. A few hatchery trout were caught up to five days after the last release.

Catches and Mesh Size

The selective action of the two mesh sizes in the bags of each net is illustrated in Figure 5. The size distribution for the catches from inside and outside bags shows the approximate minimum size each mesh caught. Owing to a gradual accumulation of algae in the meshes of both bags, some smaller fish

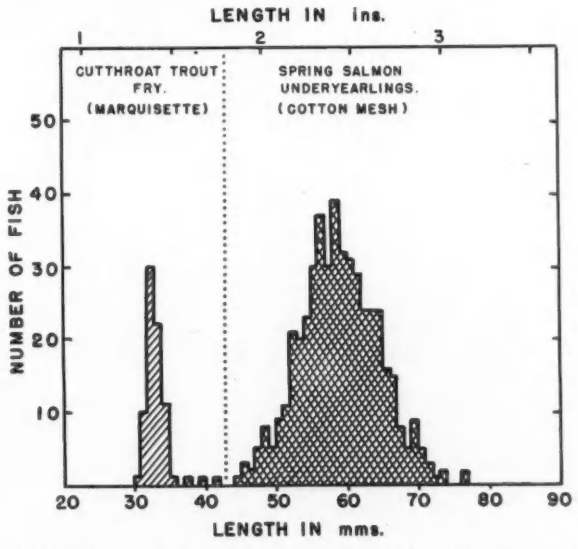

Figure 5. Size distribution of spring salmon and cut-throat trout fry by mesh size in hoop nets. The cotton mesh was ½ inch, stretched; the marquisette was of fixed opening, 4/16 by 5/16 of an inch.

were caught in a given mesh which otherwise might have slipped through. Following a full night's fishing the majority of the fish in the two bags were dead, pinned against the mesh. Lifting of the nets after shorter intervals of operation (up to four hours) during darkness, usually revealed a number of live fish, some of which, by their size, would possibly have swum out had the net remained submerged.

By the use of a lucite viewer built into the bottom of a fibreglass boat it was possible to survey the bottom of the canal and make a rough count of the number of young salmonoids holding position above the nets. Without this aid very few, if any, young spring salmon would have been observed except from net catches. To the unaided eye their protective coloration and swimming action concealed them entirely against undulating strands of green algae covering the brick surfaces. During the peak period of the catches an estimated 800 springs were scattered from depths of three to four feet over a 300-foot stretch of the canal. Over half as many were still to be observed when netting was terminated. By comparing the size of these fish with the width of the bricks over which they held position it was possible to estimate sizes up to 80 and 90 mm., too large to be caught by the hoop nets (compare Figure 5).

DISCUSSION

Different approaches may be employed to solve the problem of saving downstream migrants from destructive watercourses. Success may be achieved through methods based on *attracting*, *guiding*, *scaring* or *forced swimming* (by timed electrical discharges). Each of these is entirely different from the others and undoubtedly will have varying degrees of application in accordance with the species concerned and the prevailing environmental conditions. The importance of understanding both where and how the fish are migrating is difficult to overrate. The present work, aimed at deflecting young spring salmon, mainly through a combination of *scaring* and *guiding*, has served to illustrate these aspects, although achieving only limited success.

The subtleties of what attracts a fish are relatively obscure, as compared with the simplicity of producing scare responses. Factors associated with feeding, reproducing or promoting survival in general will probably be linked with attraction. Those creating scare responses are known to every fisherman; yet many foreign sounds, varied light patterns and water disturbances have apparently no effect or association producing any responses, as the underwater diver will testify.

The most direct approach, as mentioned in the introduction, was to attempt a mechanical reproduction of disturbances in an effort to direct fish by scare responses. This was conceived, not as a blunt block in the path of the fish, but as a deflecting agent angled downstream in the nature of a guiding factor. The bubble angle of 40° to 25° was merely a first choice. The current rate and the nature of the migration were of significance in this regard. The rapid flow in the canal and non-schooling habit of the migrating spring salmon possibly reduced the effectiveness of the guiding principle. Night observations by

momentary illumination with a flashlight revealed that some of the spring salmon moved inshore to the shallow edge of the canal and were orientated upstream. Repeated observations of the number of fish directly downstream from the hoop nets during a night's operation showed little change in the visible numbers. It appeared that only a slow downstream displacement was taking place.

The trout fry were never observed by day or night to be away from the shallow edge, and their downstream movement was more pronounced numerically. Unlike the spring salmon, the reduction in trout fry catches (Figure 4) was in keeping with reduced numbers seen along the canal.

Artificial lights have been used as an obstructive influence on the downstream migration of eels. Lowe (1952) was able to effectively prevent eel runs for periods up to half an hour, the limit of experimental tests. Sorensen (1951), while investigating the capacity of eels (7 to 30 cm.) to swim upstream against strong currents, conducted experiments at various times of day. The movement of the larger eels was mainly confined to the hours of darkness. Such findings as these help to encourage investigation of the use of light as a directing factor for other migratory fishes. It is hoped to extend the present investigation on downstream migrating salmonoids to include a schooling species, like young sockeye salmon, and to deal with slower rates of flow.

Air bubbles have been used in laboratory experiments as a barrier to upstream movements of adult fish (Bramsnaes, 1942). It is reported that "this form of barrier had a great effect on carp and pike, which could not be driven through the veil of air while the trout seemed to pass entirely unaffected".

In addition to the use of a wall of bubbles as a possible directive influence in itself, it was also the intention to beam sound into this deflection area by means of a portable echo sounder. The aim was to use a suitable combination of wave length and bubble size such that the sound pulses directed against the bubble wall from a downstream point would be reflected. Fish passing into the deflection area from upstream would be subject to a sudden increase in sound. Although little is known of the sound frequencies which salmon can detect, it is reported that fish lacking a Weberian apparatus are limited in the upper audibility range to frequencies of about 6,000 cycles per second (von Frisch, 1938). Echo sounders operate at a frequency of 16,000 c.p.s. Since more suitable equipment was not available, this apparatus was used in a preliminary experiment to test its applicability. Unfortunately it has been impossible to separate the effect of the *bulk* of the immersed sound transmitter from the factor of the *sound transmitted*. A turbulence was set up which, it was afterwards discovered, interfered with the fishing efficiency of the net, possibly allowing fish to swim out of the net as a result of a back-eddy. The data from nights which involved the sound-producing gear have therefore been set aside for present considerations; however, some observations of interest were made.

The use of an echo sounder in conjunction with the wall of bubbles was based on the concept of a stimulus, i.e. a change in intensity. Merely beaming sound into the canal from one bank would envelop the whole stream in steadily

transmitted, unconfined sound waves. This is possibly why Burner (MS) found no movement away from the sound source while experimenting with spring salmon. Using a sound-reflecting surface which was penetrable by the fish meant a sudden change for any migrants passing into and possibly scared out of the sound zone. The high frequency of the echo sounder, although perceived by the human ear, appears either to be out of the audibility range of the young salmonoids or to have no association resulting in detectable response. Switching the echo sounder on and off produced no visible response in fish within close range of the transmitter.

The ultimate aim is to direct 100 per cent of the downstream migrants into safe by-passes. Obviously lesser degrees of success cannot and should not be considered unsatisfactory. There is a lower limit of success which is still within the bounds of practical application, but which will undoubtedly vary in relation to given conditions such as the presence of a series of dams, and the economic balance of cost of installation plus maintenance and value of returns. The average success achieved with spring salmon migrants using a beam of light can be expressed as two fish deflected for every three fish approaching the net, under the conditions prevailing in the canal. A loss of 33 per cent could therefore be expected if the net opening represented an irrigation intake. Whether this is sufficient is debatable. However, further experimentation is both desirable and warranted.

ACKNOWLEDGMENTS

We are indebted to Mr. E. W. Burridge, Department of Fisheries, for directing us to, and supplying us with information on the salmon of the Puntledge River canal.

The Provincial Game Department provided the stocks of Kamloops trout fingerlings from the Puntledge River Park Hatchery. The portable echo sounder was obtained through the courtesy of Dr. F. H. Sanders of the Pacific Naval Laboratories. These contributions, and the work of Mr. K. R. Sutherland in constructing and assembling the gear, are gratefully acknowledged.

SUMMARY

Catches of downstream-migrating spring salmon in two similar hoop nets placed on either side of the Puntledge River canal indicated an even distribution of these young fish within the canal.

A significant reduction in the catch of one net was produced through the use of a deflecting beam of continuous or flashing light. The catches in the "deflected" net averaged about one-third those in the control net.

A wall of bubbles released from a submerged tube at a downstream angle of 40° to the edge of the canal did not have sufficient deflecting effect to be considered significant. In conjunction with light, however, a one-third reduction was also achieved.

Cut-throat trout fry and hatchery-cultured Kamloops trout fingerlings did not respond in the same manner as the spring salmon migrants. A current of 3 feet per second away from the edge of the canal was believed to be too rapid to permit the trout fry to swim out from the deflection zone.

Application of this technique is suggested for slower rates of flow. Comparison should be made with species which show schooling tendencies.

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A Collection of Oceanic Fishes from off Northeastern Japan

By Giles W. Mead[1] and F. H. C. Taylor[2]

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During the spring of 1952 the governments of Canada, Japan and the United States co-operated in an investigation of the fur seals in the coastal waters of Japan. The investigation centred in the waters off Miyagi and Iwate Prefectures in northeastern Honshu and was concerned with all aspects of the natural history of that part of the seal herd which habitually winters in the area. Among the studies undertaken was an analysis of the food habits of the seal, with special reference to the effect of predation on fish stocks of commercial importance to the Japanese. Early in the study it became evident that a large proportion of the seals' food consisted of lantern fishes (Myctophidae) of several species. The bony remains of these fishes (dentaries, premaxillaries, caudal skeletons, otoliths, etc.) found in the seal stomachs were readily identifiable to family, but could not be referred to the appropriate genus or species without a comparison with the same structures from positively identified specimens. The collection of this comparative material was accomplished through a series of midwater trawling operations carried out in waters in which seals were abundant. Although the facilities were not ideal and the number of successful hauls small, the results were gratifying. As well as providing the desired specimens for use in the identification of the seal stomach contents, the collection yielded distributional data of considerable interest.

A ten-foot midwater trawl of the type recently designed at Scripps Institution of Oceanography (Isaacs and Kidd, 1951) was used. The net was operated from the *Iwate Maru*, a research vessel generously provided for the purpose by the Iwate Prefectural Fisheries Experimental Station. Since no winch or wire cable was available, the net was towed by a manila rope one inch in diameter and was raised and lowered manually with the aid of the niggerhead on the anchor winch. All tows were made at a speed of four knots. Trawling operations were carried out on April 20 and May 26-27, 40 to 50 miles east by north of Ohakozaki, Iwate Prefecture, and on May 7, 65 miles east southeast of Ohakozaki.

A series of four hauls, using 30, 110, 200 and 290 meters of tow rope, was made during daylight and again after dark on the first two occasions, but only after dark on the third. The depth at which the net fished was estimated by three methods: by the angle at which the rope entered the water (the "wire angle"), from a cable profile curve, and by the use of a bathythermograph in conjunction with the net. Minimum estimates were arrived at by calculating the product of the sine of the wire angle and the length of the tow rope minus a

[1]Natural History Museum, Stanford University, California.
[2]Pacific Biological Station, Nanaimo, British Columbia.

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correction of 2.2 meters for the height of the towing point above the water line. The depths calculated from the cable profile curve formed maximum estimates since the manila rope used in our operations offered a greater resistance to the water and was lighter per unit length than the ¾-inch wire rope used in the preparation of the curve. The cable profile curve was prepared at Scripps Institution of Oceanography during field tests of the ten-foot midwater trawl. At various tow-rope lengths the ordinate shows the depth of the net; the abscissa

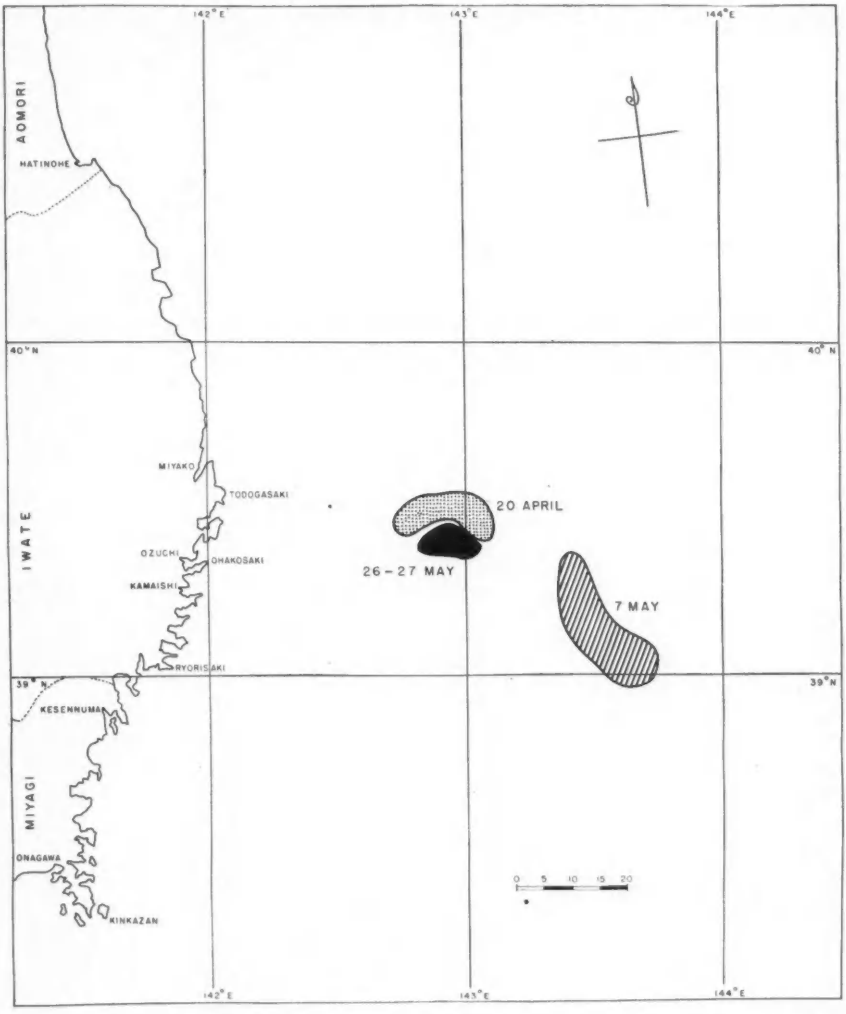

FIGURE 1. Locality of each of the three trawling operations shown with reference to the coast of northeastern Honshu.

TABLE I. Locations, depths and times of hauls.

Date	Haul no.	Location with reference to Ohakozaki	Direction of haul	Distance net towed	Amount of tow rope	Estimated depth of net	Time net towed through water
				miles	*meters*	*meters*	
April 20, 1952	1	48 miles E	SE	2	200	58–100	1242–1340
	2	50 miles E	NNW	2	290	87–140	1358–1525
	3	49 miles E	NW	1.5	110	60	1628–1720
	4	46 miles E	NW	2	30	13	1728–1820
	5	38 miles E ½ N	SW	1.5	290	failure	2032–2150
	6	36 miles E ¾ N	W/S	2	200	60–100	2223–2324
May, 7, 1952	1	75 miles ESE	S	3	30	13	0905–0953
	2	76 miles ESE	E	3	110	60	1012–1047
	3	79 miles ESE	E	3	200	54–100	1110–1217
	4	82 miles ESE	N	4	290	77–140	1237–1333
	5	68 miles E/S ¾s	N	3	290	73–140	1933–2037
	6	76 miles E/S ½s	N	3	200	50–100	2055–2152
	7	66 miles E/S ½s	N	3	110	60	2205–2248
	8	68 miles E/S	N	3	30	13	2259–2335
May 26, 27, 1952	1	45 miles E	N	4	30	13	2025–2113
	2	45 miles E/N	SW	3	110	60	2130–2225
	3	44 miles E	E	3	200	66–100	2245–2347
	4	47 miles E	W	3	290	88–140	0012–0125
	5	44 miles E	W	3	20	5.5	0143–0228

the horizontal distance between net and vessel. The tests were made at a towing speed of 4.3 knots. A third estimate was obtained through the simultaneous use of the trawl and a 450-foot bathythermograph. On the third trawling operation the bathythermograph was suspended 20 meters below the beam of the trawl on those hauls using 20, 30 and 110 meters of tow rope. For fear of damaging the pressure bellows of the instrument it was thought inadvisable to use it on deeper hauls. A test showed that at four knots the bathythermograph assumed a position 40 feet below the beam of the trawl. Depth estimates so derived are thought to be more reliable than those calculated by the first two methods. In Table I are recorded the date, location, length and duration, best estimates of depth and time of each tow.

Since the trawling operations were of very limited extent, no reliable quantitative data regarding the vertical distribution and migrations, relative number of individuals, etc., were obtained. The collection, however, has contributed appreciably to our knowledge of the distribution of pelagic species in Japanese waters.

Tanaka (1931), by listing the marine littoral species of fishes found in northern and in southern Japan, confirmed the views held by earlier authors that the point of greatest faunal change occurs off Cape Inubo (near Chose, north of Tokyo). Here the warm Kuroshio current from the south is deflected away from the shore and the colder subarctic water dominates in the coastal areas. The collections necessary to show whether or not those pelagic species frequently encountered in surface waters near the coast are similarly affected by this abrupt temperature barrier have not been made. With the exception of the limited work of the *Albatross* in northern Japan, no extensive collection of non-commercial oceanic fishes has been assembled. The distributional picture is, therefore, very misleading. For example, Kuroda (1951, p. 318, compilation) records 23 species of lantern fishes from Suruga Bay. Of these, only three are known from north of Cape Inubo, while the remainder are widely distributed south of the Cape. Past records of these species are based largely on specimens taken relatively close to shore and not at great depths. It would thus seem that these pelagic fishes conformed to the distribution of the shore forms. In our collection, however, six myctophids are represented which were unknown previously in the waters off northern Japan but are common in the south. The distribution of most members of this family has been thought to be strongly correlated with surface isotherms (see Fraser-Brunner, 1949, p. 1020). The extension of warm water of Kuroshio origin into the region in which the trawling was done, rather than the extension of the known range of warm-water species into a cold-water mass, offers the most probable explanation of this distributional phenomenon. This view is supported by the results of the analysis of the surface-water temperatures which was made during the course of the fur seal investigations.

The most complicated hydrographic conditions in the North Pacific are encountered in the waters off Aomori, Iwate and Miyagi Prefectures, Japan. Here the subarctic water carried south by the cold Oyashio meets the warm central water carried northeast by the Kuroshio. The Kuroshio follows closely

along the coast of Japan as far north as latitude 35° N., where it turns eastward, sending branches toward the northeast. Where these waters meet the Oyashio current from the north, intensive mixing takes place. The region of convergence

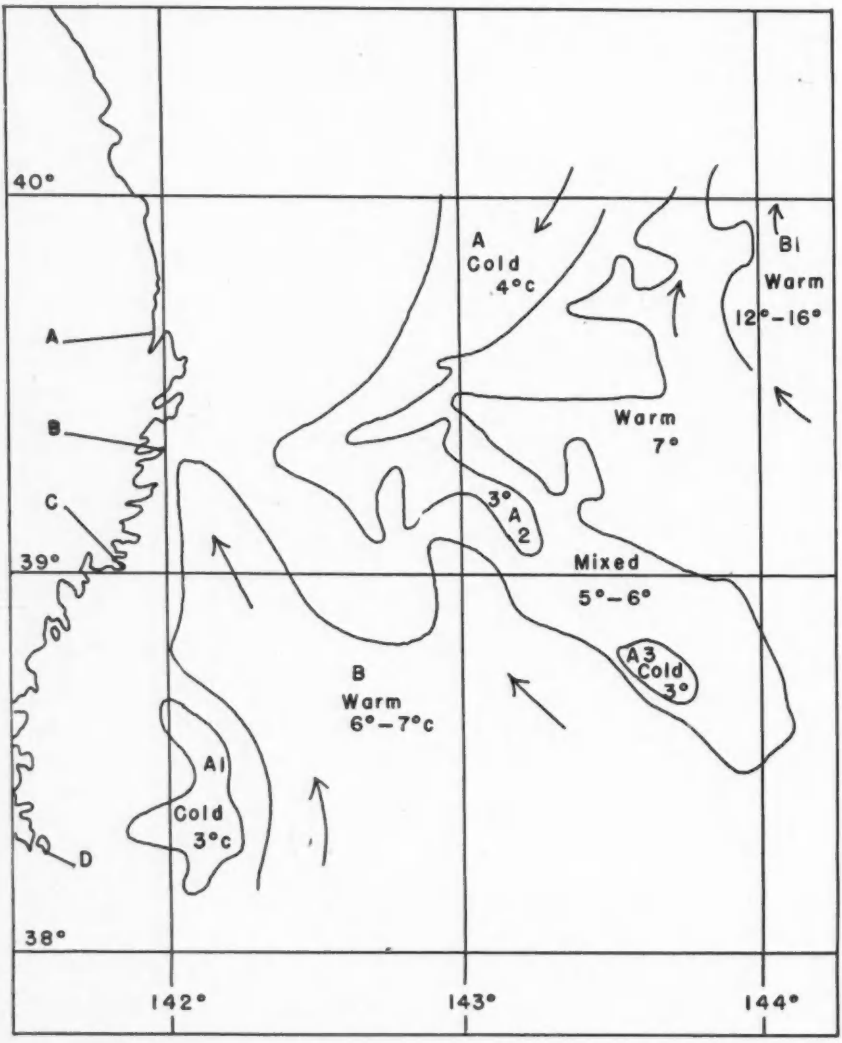

FIGURE 2. Distribution of water masses off Iwate and Miyagi Prefectures for the period from April 20–29. *Localities*: A–Miyako; B–Ohakosaki; C–Ryorisaki; D–Kinkazan. *Water masses*: A is a branch of the cold Oyashio current from the north. A_1 and A_3 are swirls of cold water cut off from the main body by the warm-water mass B. A_2 is the offshore branch of the cold system. B represents the warm-water mass cooled slightly through mixing. B_1 represents the main warm-water mass from the south.

varies with the season of the year. In winter the Oyashio extends south almost to latitude 35° N. In spring and summer, as the Kuroshio increases in strength and as the Oyashio decreases, the region of convergence is moved progressively

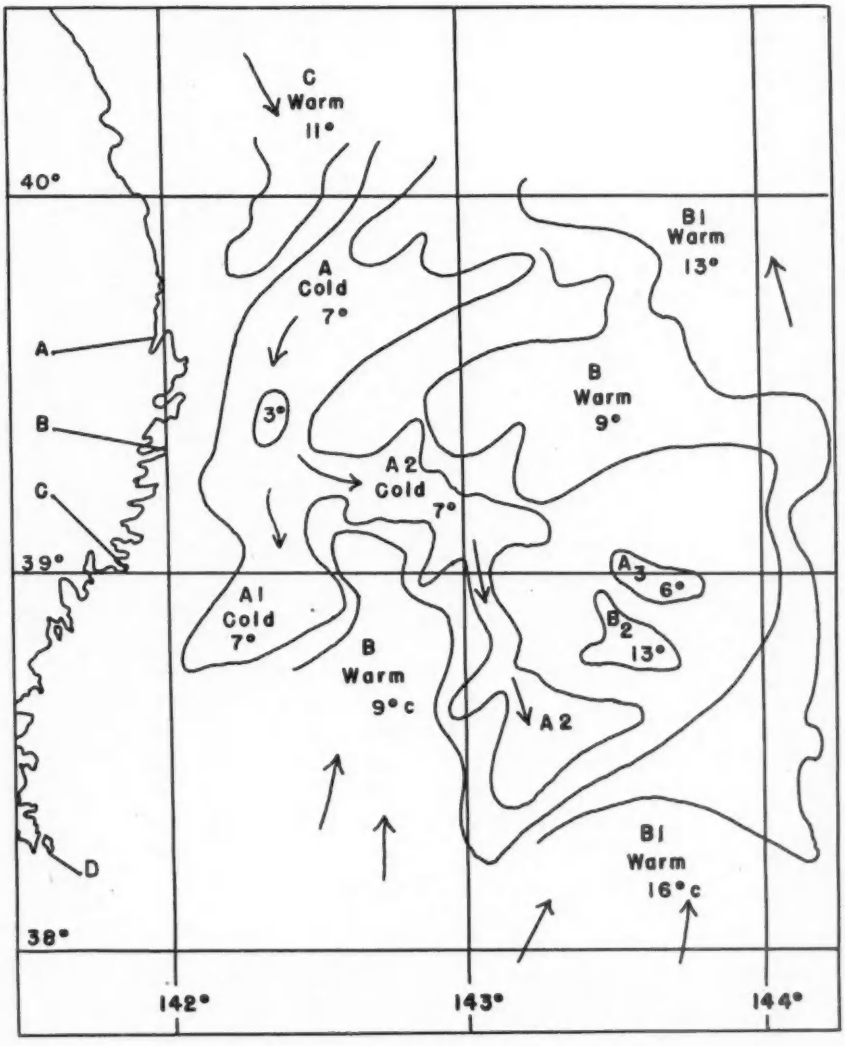

FIGURE 3. Distribution of water masses off Iwate and Miyagi Prefectures for the period May 7–10. Localities are as in Figure 2. *Water masses*: A represents the main cold-water mass; this divides into an inshore branch A_1 and an offshore branch A_2. A_3 represents a swirl of cold water cut off from the main mass. B represents part of the warm-water masses and B_1 the main warm-water mass. B_2 is a cloud of warm water cut off from the main body. C is a warm southward-moving water mass.

farther north until it is found off northern Hokkaido in midsummer. The situation is further complicated by marked and rapid shifts in the positions of the water masses.

Surface-temperature observations were made by each of the six sealing

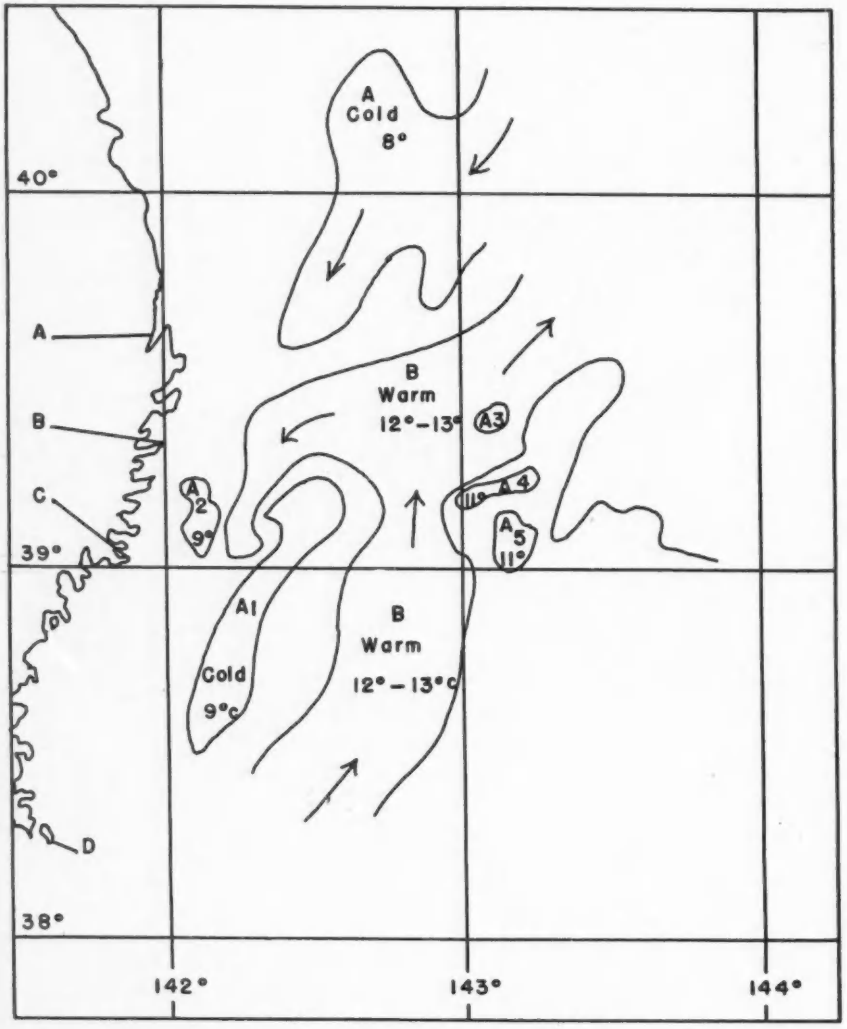

FIGURE 4. Distribution of water masses off Iwate and Miyagi Prefectures for the period May 26–31. Localities are as in Figure 2. *Water masses*: A represents the cold-water mass. A_1 to A_5 are clouds of cold water cut off from the main body. B represents the main warm-water mass.

vessels at hourly intervals and each time a seal was killed. From these readings charts of the surface-water isotherms were made for ten-day periods. These charts showed the locations of the warm and cold-water masses and the areas of mixing between them for each period.

Briefly, the changes in the hydrographic conditions that occurred in the region off Miyagi and Iwate Prefectures from March to May, inclusive, may be summarized as follows: In March, the cold water from the Oyashio system dominated the region. This water was characterized by temperatures of 0° to 3°C. During April and most of May the Kuroshio system increased in strength as the Oyashio system decreased. Intensive mixing between the two systems took place in this region. The temperature of the cold-water mass increased from 0° to 3°C. in March to 8° to 12°C. in May. By the end of May the Kuroshio system was dominant off Iwate and Miyagi Prefectures. Warm water of 13° to 14°C. spread out over most of the area. Water of the Oyashio system, now much reduced in extent, was characterized by temperatures of 8° to 9°C.

Trawling on April 20 took place in an area of intense mixing between the outer boundary of the cold-water mass and the inner boundary of the warm-water mass. In this region warm, partially mixed, water of 7° to 8°C. was intruding into the main cold mass of 4°C. The situation is illustrated in Figure 1, a simplified chart drawn from the isothermal map for the period from April 20 to 29.

The second trawling operation on May 7 also took place in an area of mixing between the warm- and cold-water masses. The region was characterized by interlocking fingers of warm and cold water. The temperature ranged from 8° to 10°C. in the immediate trawling locality but was more variable in the area as a whole. Figure 2 shows a simplified diagram of the isotherm for the period from May 7 to 10.

By the time the third trawling operations on May 26-27 were carried out, the Kuroshio system was dominant throughout the area. The cold-water mass was much reduced in extent and mixing was somewhat less intense. The hauls were made in water of 11° to 13°C. in a region where warm water of Kuroshio origin dominated; the remnants of the cold-water mass were represented by water of 8° to 9°C. and by several large swirls of water of 10° to 11°C. The conditions existing during the period between May 26 and 31 are shown in simplified diagrammatic form in Figure 3.

ENGRAULIDAE

Engraulis japonicus Temminck and Schlegel, 1846, p. 239, pl. 108: 3

A single specimen, 129.5 mm. in length, taken May 27, haul 5.

BATHYLAGIDAE

Bathylagus nakazawai Matsubara, 1940, p. 315

Twenty-three specimens collected as follows: 4 specimens, 28.1-54.2 mm. in length, taken May 7, haul 5; 1 specimen, 75.0 mm., taken May 7, haul 7; 14

specimens, 32.6-69.0 mm., taken May 26, haul 2; 3 specimens, 31.2-53.7 mm., taken May 26, haul 3; 1 specimen, 62.0 mm., taken May 27, haul 4.

Our fish are apparently the first collected since those comprising Matsubara's type material. The collection extends the known range 350 miles north of Suruga Bay, the type locality.

GONOSTOMIDAE

Maurolicus japonicus Ishikawa, 1915, p. 183, pl. 12

Fifteen specimens collected as follows: 1 specimen, 29.3 mm. in length, taken May 7, haul 7; 13 specimens, 21.1-26.6 mm., taken May 26, haul 1; 1 specimen, 22.6 mm., taken May 26, haul 3.

Our specimens, clearly referable to *Maurolicus* as characterized by Norman (1930, p. 297), Bruun (1931, p. 286) and others, represent a population distinct from those elsewhere in the oceans of the world. Norman (*op. cit.*), after comparing specimens from New Zealand, the Mediterranean and the Atlantic and following the precedent of Jordan and Hubbs (1925, p. 154), Tanaka (1931, p. 49) and others, considered *M. japonicus* to be a synonym of *M. mülleri* (Gmelin, 1789; in Linnaeus' *Syst. Nat.*, ed. 13, p. 1378). Matsubara (1938, p. 50; 1938, p. 60; etc.) recognized the Japanese species as distinct and distinguishable from the Atlantic species because it has the ventral fin inserted before the vertical of the dorsal origin as opposed to below it. During the course of development of the Atlantic *M. mülleri* the relative position of the fins varies greatly (see Jespersen and Taning, 1926, p. 40; Sanzo, 1931, p. 55, pl. 5; 1935). Primordial ventral fins make their appearance in advance of the dorsal, lie on a vertical with the dorsal origin at a length of 17 to 22 mm. and occupy a more posterior position thereafter. Fin placement, therefore, may or may not adequately differentiate the Japanese species of *Maurolicus*. A comparison of the gill-raker counts, however, confirms Matsubara's conclusion that *M. japonicus* is a distinct species. The gill-raker counts of *Maurolicus* taken at various localities (Table II) show that the total number of gill rakers on the anterior arch of the Japanese specimens is consistently below 27, while in those from other waters it is above 28. Although Norman (1930, p. 299) counted only those rakers on the lower limb of the anterior arch, it can be assumed that the total count would have been greater than 28, since the number of ceratobranchial rakers in his non-Japanese specimens was at least two higher than in any of the Japanese material. *M. japonicus* is known from Uodu, Ettyu, Sea of Japan and off the Idu Peninsula on the Pacific side of Japan (Ishikawa, 1915, p. 189) and from off Kambara in Suruga Bay (Matsubara, 1941, p. 2). Hitherto the species was unknown north of Cape Inubo.

Gonostoma gracile Günther, 1878, p. 187

Eighty-five specimens collected as follows: 2 specimens, 26.0 and 35.5 mm. in length, taken May 7, haul 5; 35 specimens, 33.1-69.0 mm., taken May 26, haul 2; 41 specimens, 32.2-82.4 mm., taken May 26, haul 3; 7 specimens, 42.0-99.1 mm., taken May 27, haul 4.

TABLE II. Gill-raker, anal and postanal photophore counts of Japanese and non-Japanese *Maurolicus*.

Authority or specimen	Size of specimen(s)	Gill-raker counts			Anal photophores[a]	Postanal photophores
		Epibranchial	Ceratobranchial	Total		
	mm.					
Norman, 1930 (various non-Japanese localities)	20–52		25–27		15–18	8–9
McCulloch, 1923 (Australia)					15–17	8–9
S. U. 9572 (Messina)	40.9	7	23	30	14	7
	38.4	7	22	29	16	8
Ishikawa, 1915 (Japan)	43–51			24	15	8
S. U. 23544 (Japan)	40.5	7	18	25	14	8
	40	7	19	26	14	8
May 7, 1952, haul 7	29.3	7	19	26	15	8
May 26, 1952, haul 1	25	6	19	25	14	8
	23	7	18	25	14	8
	22.2	6	17	23	14	8
	21.4	7	19	26	14	9
	24.3	7	18	25	14	8
	21.1	6	19	25	14	8
	26.6	6	17	23	14	8
	23.2	7	18	25	15	8
May 26, 1952, haul 3	22.6	8	18	26	15	8

[a]Exclusive of the initial elevated organ.

Our specimens agree well with the descriptions of Günther (1878, p. 187; 1887, p. 174, pl. 45: C), Norman (1930, p. 282) and Matsubara (1938, p. 41).

Rass (1950, p. 1042) distinguishes his *Gonostoma vitiazi* (from 300-360 miles southeast of Urup Island, Kurile chain) from *G. gracile* "because of the presence of the upper rows' six photophores widely spaced out along the spine". We find no significant differences between the photophore pattern, or other characters, of his type description and Norman's redescription of the types of *G. gracile* (1930, p. 285) or that of Matsubara's specimen (1938, p. 41).

We see no reason for retaining the generic name *Neostoma* applied to this species by the contemporary Japanese workers. If *Neostoma* is to include *N. bathyphyllum* Vaillant (1888, p. 96, pl. 8: 1) and *G. gracile* Günther, as suggested by Jordan and Starks (1904, p. 580), it must be enlarged to include *G. elongatum* as well, since the species of *Gonostoma* exclusive of *G. denudatum* Rafinesque form a more natural species cluster (Norman, 1930, p. 282). Norman's inclusion of all these nominal species in the genus *Gonostoma* seems to be a natural arrangement more consistent with the classification of other gonostomid groups.

Previously known from south of Japan (type locality), from Suruga Bay (Jordan and Starks, 1904, p. 579), from Kumano-Nada southeast to the Kii Peninsula (Matsubara, 1938, p. 41) and from off Urup Island (*G. vitiazi*).

STERNOPTYCHIDAE

Sternoptyx diaphana Hermann, 1781, p. 33

Twelve specimens, 18.5-41.4 mm. in length, collected May 3, 1952, about 40 miles off Iwate Prefecture by Mr. Karl W. Kenyon aboard the *Geizan Maru*. Numerous fish of this species were seen floating dead on the water. All of

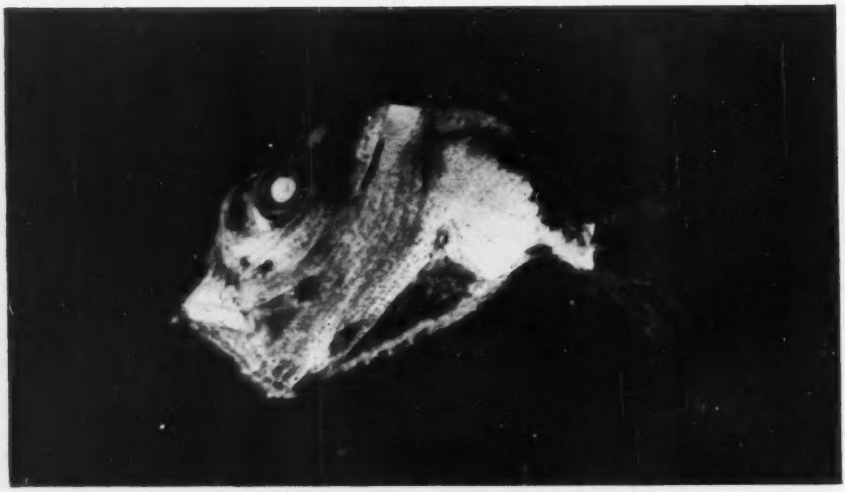

FIGURE 5. *Sternoptyx diaphana*, 37.5 mm. in standard length.

our specimens are of the type figured by Günther (1887, pl. 45: D′), those forms in which a strongly protruding chin and steeply inclined forehead cause the anterior profile to resemble more closely a gentle curve than an obtuse angle with the point at the mouth. The only previous record of this species in Japanese waters is that of Jordan and Snyder (1900, p. 350), which was based on specimens "killed by earthquake and captured floating" off eastern Hokkaido.

STOMIATIDAE

Opostomias mitsuii Imai, 1941, p. 239

Our single specimen, 61.6 mm. in length, taken May 26, haul 2, is the second known representative of the species.

Three species of Günther's genus *Opostomias* are currently recognized: *O. micripnus* (Günther, 1878, p. 180; 1887, p. 208, pl. 53: A), *O. gibsonpacei* Barnard (1948, p. 345, figs. 1-2) and *O. mitsuii* Imai (1941, p. 239). The first of these is known from Australia, the second from South Africa and the third from Japan. The species can be distinguished as follows:

(*a*) Pupil vertically elliptical; eye small, 6-7 in length of head; branchiostegal rays 15. *O. micripnus*

(*aa*) Pupil circular; eye large, less than 6 in length of head; branchiostegal rays 10-11.

(*b*) Anal fin with 22-24 rays; ventral fin long, over twice the length of the head; head about 5-6 in length. *O. mitsuii*

(*bb*) Anal fin with 25-26 rays; ventral fin short, about equal to length of head; head about 8-9 in length. *O. gibsonpacei*

With due allowance for its smaller size, our specimen agrees well with the description of Imai's type, which was collected off Manazuru in Sagami Bay. In our fish the eye is relatively larger, the dorsal rays more numerous (23 *cf.* 21), the anal rays fewer (22 *cf.* 24) and the dentition stronger. Each half of the premaxillary bears seven strong teeth. Of these the second (the largest) and the fifth are depressible. Imai (1941, p. 239) reported: "Premaxillary with 4 outer fixed teeth, the second long, its length about two-thirds of eye, with 1 long inner depressible tooth; the first, the third and the last teeth moderate, with 1 or 2 depressible teeth". Both Imai's specimen and ours bear a pair of fangs on each side of the vomer. The maxillary and the mandibular dentition of the two specimens is similar. The appreciable amount of variation between Barnard's two type specimens of *O. gibsonpacei* leads us to conclude that the differences in dentition, proportion and extent and shape of the mandibular barbel between the two known specimens of *O. mitsuii* are due to interspecific variation and ontogenetic changes. The capture of our specimen extends the known range more than 350 miles to the north.

Fin formula: D. 23, A. 22, P. 1-4/1-4, V. 7.

Measurements, in thousandths of standard lenght (61.6 mm.):

Length of head	167	Least depth of caudal peduncle	26
Length of snout	49	Snout to origin of dorsal	792
Diameter of eye	52	Snout to origin of anal	805
Length of postorbital	81	Snout to origin of pectoral	164
Width of bony interorbital	49	Snout to origin of ventral	580
Length of maxillary	130	Length of dorsal base	148
Length of mandible	138	Length of anal base	133
Length of mandibular barbel	136	Length of pectoral fin	156
Greatest depth of head	122	Length of ventral fin	65
Greatest depth of body	71	Length of mid-caudal ray	41

Tactostoma macropus Bolin, 1939, p. 39

Although agreeing in most respects with the description of *Tactostoma macropus* (Bolin, 1939, p. 39; = *Photonectops multipunctata* Chapman, 1939, p. 515) our two Japanese specimens show several distinguishing features worthy of comment here.

Our specimens show higher dorsal and anal counts (Table III) than those reported from the eastern Pacific. Noteworthy differences in number of teeth and rows of teeth are also apparent. Since material for a study of the developmental changes is not available, we tentatively ascribe these differences to that cause.

TABLE III. Fin-ray and tooth counts of specimens of *Tactostoma macropus* from California, British Columbia and Japan. Data on the 71-m. specimen, the holotype, from Bolin, 1939, p. 39. The two British Columbia specimens are those reported by Chapman, 1939, p. 516, the type and paratype respectively of "*Photonectops multipunctata*".

	California		British Columbia		Japan	
Standard length (mm.)	71	194	280	99	266	287
Dorsal	16	16	16	14	17	17
Anal	20	19	19	19	22	21
Ventral	10	9/9	9/10	8/8	9/9	9/9
Rows of dentary teeth	11	11/11	11	9	14/14	13/14
Number of teeth in each half of upper jaw	36	47/45	21	30	58/53	45/47
Number of teeth in each half of lower jaw	54	58/60	85	45	77/74	81/86

The size and placement of the luminous glands on the head also vary between specimens from the two widely separated localities. A luminous gland is present on the dorsal midline of the head of the two California specimens examined, the holotype of *T. macropus* and a second specimen collected just outside Monterey Bay (*Tage* station 133B). The size of the gland is about half that of the pupil of the eye and it lies on a line drawn across the top of the head from the anterior margins of the orbits. In the Japanese specimens this spot is very poorly defined, being surrounded and to some degree surmounted by extensions of the heavily pigmented skin. The large elongate light organ below the eye extends horizontally from a vertical with the anterior margin of the eye to a point below the posterior margin of the pupil in the California specimens (especially in the larger), but in the Japanese representatives it occupies a position below the anterior half of the pupil. The preorbital glands of all specimens are similar. Unfortunately the skin of both Japanese specimens was lost during capture, making a direct comparison of the body photophores impossible.

The structure and number of gill rakers may prove of phylogenetic importance when larger numbers of specimens can be examined. In the California specimens the rakers are reduced to clusters of teeth, three to five at each locus, in a manner reminiscent of some members of the Paralepididae. There is one such cluster on the epibranchial; 10-11 on the ceratobranchial. In

our Japanese material the epibranchial is naked and the teeth of the gill rakers of the ceratobranchial form clusters far less easily distinguishable from one another than those of the California specimens. Until specimens from intervening localities have been examined, it seems best to refer the Japanese material to *T. macropus*—a range of extension of over four thousand miles.

TABLE IV. Proportional measurements, expressed in thousandths of standard length, of specimens of *Tactostoma macropus* from California and Japan. Data on the first specimen, the 71-mm. holotype, from Bolin, 1939, p. 40.

	California		Japan	
Standard length (mm.)	71	194	266	287
Diameter of orbit	20	16	21	18
Length of head	114	105	16	109
Length of snout	27	22	24	30
Length of maxillary	92	87	90	83
Length of lower jaw	103	96	96	93
Depth behind head	54	41	50	37
Greatest depth	90	50	75	60
Dorsal to anal origins	48	43	57	53
Least depth caudal peduncle	25	18	17	15
Snout to ventral origin	655	644	646	658
Snout to dorsal origin	837	866	876	874
Dorsal base	93	87	99	88
Snout to anal origin	834	861	863	864
Length anal base	121	84	91	94

MYCTOPHIDAE

The waters trawled proved to be exceptionally rich in both number and species of lantern fishes. The number and size range of the species encountered in the individual hauls are recorded in Table V.

Myctophum affine Lütken, 1892, p. 32

Previously known from Japanese waters south of Sagami Bay (Kuroda, 1951, p. 319) and elsewhere throughout the major oceans of the world.

Myyctophum californiense Eigenmann and Eigenmann, 1889, p. 124

Known from Hokkaido to Suruga Bay in Japan (Kuroda, 1951, p. 319) and from British Columbia to the United States-Mexican border in the eastern Pacific (Bolin, 1939, p. 108). We find no consistent differences between our specimens and comparative material from off California.

Myctophum asperum Richardson, 1844-48, p. 41, pl. 27: 13-15

In addition to the three specimens trawled, a fourth was collected with an electric light and dip net by Mr. Karl W. Kenyon 60 miles east of Ryorazaki, Iwate Prefecture. Here again the collection of our specimens extends the known range of the species in Japanese waters about 350 miles to the north.

TABLE V. Number of specimens, size range and collection data of the myctophids trawled. Opposite the name of the species is the number of individuals; below this number is the size range in millimeters. Omitted from this tabulation are two specimens which were not identifiable because of size and condition. Also omitted are specimens taken other than by trawling.

Date (1952):	April 20	May 7	May 7	May 7	May 26	May 26	May 26	May 27	May 27
Haul no.:	4	5	7	8	1	2	3	4	5
Time:	1736–1820	1925–2037	2201–2248	2255–2335	2023–2113	2125–2225	2235–2347	0001–0125	0140–0228
Est. depth:	13 m.	73–140 m.	60 m.	13 m.	13 m.	60 m.	66–100 m.	88–140 m.	5.5 m.
Lampanyctus leucopsarus			20 (42.7–83.5)		2 (58.5–71.2)	17 (29.3–69.0)	5 (49.4–66.7)	9 (35.4–69.5)	1 (57.2)
Lampanyctus festivus		3 (36.6–45.0)					2 (27.2–30.6)		
Lampanyctus jordani						1 (49.1)	1 (57.6)	1 (54.1)	
Ceratoscopelus townsendi			6 (25.0–74.1)		3 (36.9–84.1)				6 (39.0–83.5)
Myctophum californiense			1 (73.5)						2 (96.5–97.2)
Myctophum asperum									2 (39.4–64.4)
Myctophum affinis			1 (27.9)						
Tarletonbeania taylori			1 (67.4)				1 (33.6)	1 (30.4)	1 (68.0)
Diaphus nanus	2 (51.4–58.9)	2 (58.8–73.0)	8 (29.0–71.1)		11 (27.6–48.9)	8 (27.6–87.2)	3 (20.9–84.9)	9 (29.6–82.0)	
Diaphus latus				1 (35.4)			1 (34.6)		
Notoscopelus japonicus		2 (118.0–122.6)	1 (30.7)	2 (26.9–30.1)	9 (27.1–119.7)		2 (31.6–120.2)	1 (121.2)	1 (114.1)
Notoscopelus resplendens		1 (85.6)	2 (24.6–32.8)						

Tarletonbeania taylori Mead, 1953, p. 105

The four specimens trawled and an additional two otherwise collected constitute the type material of this species.

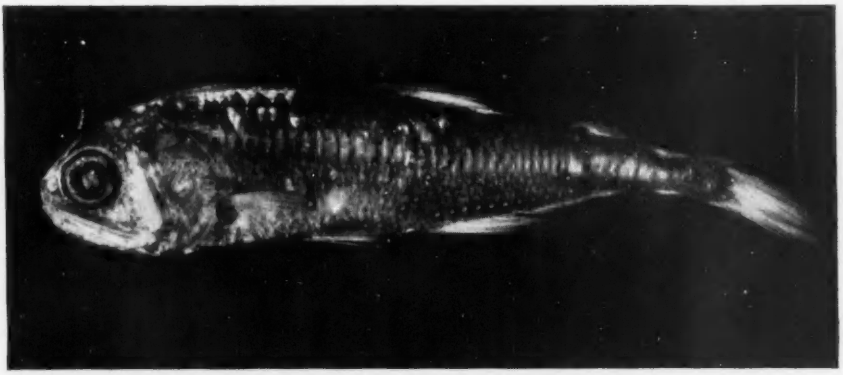

FIGURE 6. *Tarletonbeania taylori*, 68.0 mm. in standard length (holotype, U. S. National Museum No. 164970).

Diaphus nanus Gilbert, 1908, p. 224, pl. 1

Forms closely related to this species (see Bolin, 1946, p. 144) occur in the temperate and subtemperate waters of the Pacific, Atlantic and Indian Oceans and in the Mediterranean Sea (Bolin, 1939, p. 127). It has been reported from Japanese waters south of Suruga Bay (compilation of records by Kuroda, 1951, p. 319).

Diaphus latus Gilbert, 1913, p. 95, pl. 13: 1

Previously reported from Suruga and Sagami Bays (Jordan and Thompson, 1914, p. 213; Jordan and Hubbs, 1925, p. 156).

Ceratoscopelus townsendi (Eigenmann and Eigenmann, 1889, p. 125)

Ceratoscopelus townsendi, apparently one of the more common Pacific myctophids, occurs throughout southern Japan, from British Columbia to the United States-Mexican boundary in the eastern Pacific (Bolin, 1939, p. 108) and off the Marquesas Islands (Gilbert, 1908, p. 230). We have been unable to find significant differences between eastern and western Pacific specimens.

Lampanyctus leucopsarus (Eigenmann and Eigenmann, 1890, p. 5)

Another fish new to the fauna of Japan is *Lampanyctus leucopsarus*, a species hitherto known from San Diego, California, north to the eastern part of the Bering Sea (Bolin, 1939, p. 132). Since *L. beringensis* Schmidt (1933, p. 131) is apparently a synonym of *L. leucopsarus*, this range can be extended across the Bering Sea to Cape Severny on Bering Island (Commander group). Our 59 specimens are the first reported from the western North Pacific south of Schmidt's type locality—a range extension of about 1,800 miles.

Coexisting with *Lampanyctus leucopsarus* throughout most of its range and closely allied to it is *L. nannochir* (Gilbert, 1890, p. 51), a species reported from

Point Arena, northern California, to off Sakhalin in the Okhotsk Sea (see Bolin, 1939, p. 135; Schmidt, 1950, p. 55). Our Japanese specimens possess the four VO photophores, four Prc photophores and larger eye (70-87 thousandths of standard length with a mean of 77; 53 specimens measured) by which *L. leucopsarus* can be distinguished from *L. nannochir*. In no significant respects do our specimens differ from comparative eastern Pacific material.

Lampanyctus festivus Tåning, 1928, p. 67

The identity of the species cluster centring around *Lampanyctus macropterus* (Brauer, 1906, p. 239), which includes the Atlantic *L. festivus* Taning (1928, p. 67) and *L. septilucis* Beebe (1932, p. 68) and the Japanese *L. bensoni* (Fowler, 1934, p. 286), is too poorly known to enable us to refer with certainty our specimens to any of these nominal species. The key characters used by Fraser-Brunner (1949, p. 1087) to separate *L. festivus* from *L. bensoni* seem inadequate, since in our specimens the position of the VLO photophore varies from midway between pelvic base and lateral line to much nearer the latter, and the elevated fourth PO photophore varies from slightly behind the third to a little in advance of the fifth photophore of the PO series. In *L. bensoni*, however, the third Prc photophore lies midway between the second and fourth organs of the series (Fowler, 1934, p. 283, fig. 46) unlike the widely separated third and fourth Prc in *L. festivus*. For this reason alone we tentatively ascribe our fish to the North Atlantic *L. festivus*.

Lampanyctus jordani Gilbert, 1913, p. 104, pl. 14

Closely allied to *Lampanyctus festivus* but differing, among other characters, in the placement of the AOa series of photophores is *L. jordani*. The species has been known previously from the three types, collected off southern Hokkaido by the *Albatross* and from specimens collected off Kumano-Nada, southern Honshu (Matsubara, 1938, p. 56). Our three specimens agree with the type description as emended by Matsubara.

Notoscopelus resplendens (Richardson, 1848, p. 42, pl. 27: 16-18)

Our specimens of *Notoscopelus* were identified through the use of a manuscript key prepared and made available to us by Dr. Rolf L. Bolin. We

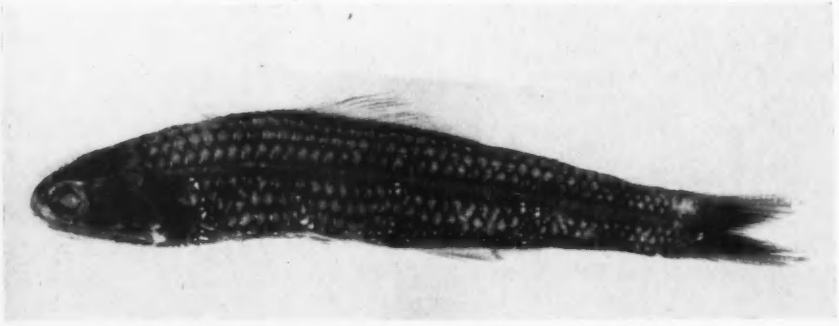

FIGURE 7. *Notoscopelus japonicus*, 119.0 mm. in standard length.

leave to his forthcoming work a discussion of the relationships, distribution and synonymy of the Japanese species. Not previously known from Japanese waters.

Notoscopelus japonicus (Tanaka, 1908, p. 5, pl. 1: 3)

Although hitherto unreported from waters off northern Japan, representatives of this species were common in the trawled collections. This species constitutes over 65 per cent of the diet of the fur-seal herd wintering off northeastern Japan. It was found in the stomachs of seals killed as far north as Erimozaki, Hokkaido. Previously known from Tokyo Bay to Shikoku (Matsubara, 1938, p. 53; Kamohara, 1952, p. 19).

SCOPELARCHIDAE

Scopelarchus linguidens Mead and Böhlke, 1953, p. 241

The three juveniles trawled have been discussed in the type description.

PARALEPIDIDAE

Notolepis coruscans (Jordan and Gilbert, 1881, p. 141)

A single specimen, 75.1 mm. in length, taken May 7, haul 7.

The capture of this juvenile specimen extends the known range of the species over 4,000 miles, from the Pacific coast of North America (Welander, 1941, p. 117) to northern Japan, and may prove to represent a population subspecifically or even possibly specifically distinct.

Greatest depth of body at nape, 17.9 in standard length, 4.1 in length of head. Dorsal and ventral profiles tapering evenly to the moderately slender caudal peduncle. Depth at origin of dorsal 5.5 in head; least depth of caudal peduncle 10.7 in head. Ventral carina not developed in our specimen. Anus situated a distance behind the origin of ventral fin equal to 0.5 the length of the fin itself.

Head elongate, its greatest depth, behind eye, equal to depth of body at nape; its greatest width 6.0 in length of head, 1.5 in depth. Snout pointed, the jaws co-terminal. Tip of lower jaw elevated and received in a concavity formed by the premaxillaries. Snout long, 2.1 in head. Nostril situated about 0.8 of orbital diameter before the anterior orbital rim. In our specimen both eyes have been lost. The orbit is large and is contained 5.7 times in head. The dorsal margin of the orbit enters into the dorsal profile of the head; the interorbital is largely flat, although slightly concave between the ridges of the frontal bones. The centre of this shallow concavity is on the midline. Postorbital length long, 1.3 in snout, 2.7 in head. All bones of the head are poorly ossified and delicate. Gape terminating under nostril when mouth is open. Dentary extending to anterior margin of orbit. Dentition incompletely developed. Each half of the premaxillary bears four depressible canines anteriorly, followed by 18 non-depressible saw-like retrose teeth. Those in the mandible are all depressible; the two nearest the symphysis are minute. Following these is the largest mandibular tooth, about equal in length to the anterior premaxillary canines and slightly recurved. Immediately following it are two minute depressible teeth followed by a toothless interspace about equal to the horizontal diameter of the nostril. Following this interspace are about ten teeth of unequal size and spacing. The posterior 0.6 of the dentary is smooth. Each palatine bears an enlarged depressible fang anteriorly and a uniserial row of about 18 minute teeth behind it. The vomer bears a patch of extremely short conical teeth which may or may not be depressible. The right anterior gill arch was cleared and stained. Five + 18 rakers in various stages of development are evident.

Dorsal fin originating at posterior end of middle third of body; distance from snout to origin of dorsal 1.5 in length; base of fin short, 7.1 in head; length of longest dorsal ray 4.3 in

head. Anal inserted midway between origin of dorsal fin and lower procurrent rays of the caudal; distance from snout to origin of anal 1.2 in length; fourth or fifth anal ray longest, 4.2 in length of head; length of anal base 6.1 in standard length. Caudal forked, the lobes equal in length; length of median caudal ray 1.5 in length of longest ray of either lobe. Pectoral fin inserted low; distance from snout to insertion of pectoral 4.3 in length; the fin relatively long, 2.7 in head. Ventral fins inserted behind the end of dorsal base, the inner edges of their insertions bordering the midline; snout to insertion of ventrals 1.4 in length; length of ventral fin 7.1 in length of head.

Black melanophores on top of head, around orbit and nostril, on tip of snout, along jaws and on the membrane joining the lower edges of the dentaries. Peritoneum marked by eight blocks of black pigment which are visible through the body wall. Below them are a few small melanophores. Between these black peritoneal areas and the lateral line the body, anterior to the insertion of the dorsal fin, is colourless. Above the lateral line the body bears scattered melanophores anteriorly. This pigmentation becomes heavier posteriorly and spreads downward. At the level of the ventral fin this stippling extends below the lateral line, covering the entire side of the body although remaining heavier dorsally. Along the entire dorsal midline of the body is a narrow band, about 0.12 mm. in width, which remains colourless. The fins are largely colourless, bearing only an occasional melanophore interradially.

Fin formula: D. 11, A. 31, P. 10-11, V. 9-10. Lateral line about 60, incompletely developed.

Measurements, expressed in thousandths of standard length (75.1 mm.):

Length of head	228	Snout to origin of adipose	931
Length of snout	110	Snout to origin of pectoral	234
Length of maxillary	86	Snout to origin of ventral	698
Diameter of orbit	40	Origin of dorsal to origin of anal	188
Width of bony interorbital	21	Origin of dorsal to origin of pectoral	405
Length of postorbital	84	Origin of dorsal to origin of ventral	292
Anterior margin of orbit to nostril	25	Origin of pectoral to origin of ventral	465
Depth of body at nape	56	Origin of ventral to origin of anal	106
Depth of body at origin of dorsal	41	Length of dorsal base	34
Least depth of caudal peduncle	21	Length of longest dorsal ray	53
Length of caudal peduncle	41	Length of anal base	165
Snout to origin of dorsal	645	Length of longest anal ray	60
Snout to origin of anal	806		

Luciosudis harryi Mead, **new species**

Holotype. A specimen 38.4 mm. in length collected on May 7, 1952, haul 5. The type will be deposited in the collection of the U. S. National Museum.

In general form our specimen agrees with Fraser-Brunner's type description of *Luciosudis normani* (1931, p. 220). Length of head 4.3 in standard length; greatest depth of head 3.0 in its length. Snout broad, 3.1 in length of head. Lower jaw extending slightly beyond upper. Gape extending to or slightly beyond anterior margin of orbit. Nostril midway between tip of snout and eye. Orbit, eye and iris horizontally elliptical; lens round. Orbit 3.5 in length of head, 2.4 in orbit. Interorbital broad and flat, 8.2 in length of head. Upper margin of orbit entering into dorsal profile. Premaxillary toothed nearly to its anterior extremity. Teeth small, numerous and irregular both in size and placement. No canines. Mandibular dentition in two series. The outer extends from the symphysis to the end of the first third of mandible and is composed of teeth which are larger than those in premaxillary, slightly recurved inwardly, and not included within the upper jaw when the mouth is closed. The inner series, a broad band, extends nearly to the angle of the gape and consists of small, conical and slightly recurved teeth. Vomer with a uniserial transverse band of minute denticles. Palatines

with a few small teeth anteriorly. Tongue toothless. Gill rakers slender and nearly smooth; 2 + 18 on anterior arch. Longest raker about equal to diameter of eye lens.

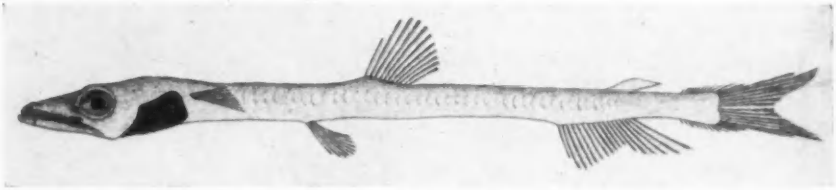

FIGURE 8. *Luciosudis harryi*, new species. Drawn from the holotype, 38.4 mm. in standard length.

Dorsal fin inserted in middle third of body, its second and third rays longest, the second through the seventh rays extending well beyond last ray when fin is depressed; distance from snout to origin of dorsal 2.0 in standard length; base of fin 3.8 in length of head. Adipose fin well developed, its length equal to that of the longest anal ray. Length of anal base 8.4 in standard length, the distance from snout to its origin 1.3 in standard length. Distance from tip of snout to origin of pectoral 4.2 in standard length; pectoral insertion about midway between dorsal and ventral midlines of body. Length of pectoral fin 2.6 in length of head. Distance from snout to ventrals 2.4 in standard length; the bases of the ventrals of either side meet posteriorly but are not confluent across midline. Length of ventrals 3.0 in length of head. Anus located at a distance behind the ventral bases equal to the horizontal diameter of the iris.

Body coloration dusky, the brown melanophores more dense above than below. Head more heavily pigmented, especially on snout and gill flap. With the exception of the caudal, which bears a few melanophores proximally, the fins are colourless.

Fin formula: D. 11; A. 17; P. 10/10 V. 10/10. Neither the scales nor the lateral line pores are sufficiently developed to permit reliable counts.

Measurements, in thousandths of standard length (38.4 mm.):

Length of head	234	Snout to origin of anal	754
Depth of head	81	Snout to origin of adipose	827
Length of snout	75	Snout to origin of pectoral	237
Horizontal diameter of orbit	68	Snout to origin of ventral	419
Horizontal diameter of eye	55	Origin of dorsal to origin of ventral	94
Interorbital (bony)	29	Origin of dorsal to origin of anal	270
Postorbital length	101	Origin of pectoral to origin of ventral	174
Length of maxillary	91	Length of base of dorsal	62
Length of mandible	135	Length of base of anal	120
Depth of body behind nape	73	Length of pectoral	88
Depth of body at dorsal origin	55	Length of ventral	78
Least depth of caudal peduncle	42	Length of median caudal ray	65
Length of caudal peduncle	117	Length of each caudal lobe	159
Snout to origin of dorsal	500		

Of this hitherto monotypic genus only a single specimen, Fraser-Brunner's type of *Luciosudis normani* has been recorded in the literature. It was collected in the South Atlantic off French Equatorial Africa. Mr. N. B. Marshall of the British Museum kindly re-examined this type for us and has forwarded counts and measurements to supplement the type description. Our Japanese

specimen differs from *L. normani* in number of anal and pectoral fin rays (17 and 10 respectively *cf.* 19 and 13 in *L. normani*), its shorter head (234 *cf.* 290 thousandths of standard length), its narrower interorbital (29 *cf.* 39 thousandths), its shorter snout (75 *cf.* 118 thousandths) and in the possession of minute teeth on the vomer and palatines (*cf.* none in *L. normani*). The other morphometric and meristic characteristics of the two specimens are similar. Since the type specimens of *L. harryi* and *L. normani* are similar in size (38.4 and 46.5 mm. respectively), these differences are of sufficient magnitude to indicate that the specimens are representatives of distinct species.

Named after Dr. Robert R. Harry, in recognition of his work on the fishes of the order Iniomi.

LEPIDOPODIDAE

Benthodesmus tenuis (Günther, 1877, p. 437; 1887, p. 37, pl. 7: B)

A single juvenile specimen, 146.0 mm. in length, collected on April 20, haul 4. Previously known only from Günther's type, which was taken off Inoshima, at a depth of 345 fathoms. *Lepidopus aomori* Jordan and Starks (1901, p. 303), based on two dried specimens, 6 and 8 feet in length, may prove to be a synonym of this species.

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The Ultraviolet Spectrum and Basicity of "Acid-Soluble" Chitin

By Howard K. Zimmerman, Jr.
Department of Chemistry, Agricultural and Mechanical College of Texas

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ABSTRACT

The spectrum of the acid-soluble fraction of chitin is determined in dilute hydrochloric acid. It is found that the chitin forms a proton adduct whose equilibrium constant is approximately calculated from the spectral data.

The constant for the proton adduct is carefully determined by a titration method, and its relation to some of the structural features of the molecule is indicated.

It appears from the literature that most recorded research on the physicochemical properties of chitin has been confined to the investigation of its properties in the solid or semi-solid state. Thus, the spectra of chitin for both ultraviolet(5) and infrared(7) light have been reported for samples in the solid condition, but not for chitin in solution. Similarly, the refractive properties of the solid material have been reported by several investigators(2), but no mention is made of these properties in solution.

The literature reports (8) that chitin is somewhat soluble in mineral acids, although not in alkali however concentrated, but this is disputed by Meyer and Wehrli(6), who indicate that the dissolution of the substance in strong acids, even at room temperature, is accompanied by hydrolytic degradation. However, since the results quoted by these writers are confined to dissolution in rather concentrated acid media, the question of possible degradation in dilute acids is still open. Without considering this possibility directly, it was thought to be of interest to attempt the determination of some of the physical properties of the acid-soluble fraction of chitin in dilute acid solutions and, if possible, to compare the determinations with those on record for the solid substance, since the fact that some of the substance does actually dissolve is beyond dispute. Although "chitin" in aqueous acidic solution is colourless in the visible region, the existence of the prior data on the ultraviolet transmission of solid chitin(5) made it appear that a study of this property in solution might lead to interesting results. The spectral study was therefore chosen as the starting point for a proposed investigation of the physical properties of acid-soluble chitin and its derivatives.

EXPERIMENTAL

The chitin used in this work was derived from crab shell.[1] The acid-soluble fraction was obtained by dissolution in hydrochloric acid, filtration, neutralization

[1]The chitin was very kindly supplied by the Research Laboratory of Bioproducts Oregon Ltd., Warrenton, Oregon.

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of the filtrate with a slight excess of sodium hydroxide, filtration to recover the chitinous material thrown down in this process, and washing with distilled water to remove alkali. It is probably best to classify this fraction as a "denatured chitin", and all references to "chitin" hereafter will apply to such a material.

The general procedure for preparing solutions was to dissolve a weighed amount of chitin to volume in standard 0.0886 M HCl. (The chitin will not dissolve in acid much more dilute than this, although once dissolved, it will remain in solution until the acid is almost entirely neutralized by alkali.) Stock solutions containing from one to two grams of chitin per liter were prepared in this manner, and other solutions were prepared by dilution with the acid solvent. Concentrations herein are given on the basis of the weight of the acetylglucosamine repeating unit of chitin (on the assumption that hydrolysis of the acetyl group is negligible), and they therefore reflect molar concentrations of nitrogen.

The instrument used in the spectral portion of the work was a Beckman Model DU Quartz Spectrophotometer.

The spectral observations disclosed a definite basicity effect attributable to the chitin. Titration of chitin solutions with alkali confirmed this effect. It was observed that, upon titration of the acid solution, a white precipitate of chitin occurred (which we shall term the "chitin end point") before the point of acid equivalence (acid end point) as indicated by phenolphthalein was reached. If about 30 ml. of chitin solution are used for titration, the two end points are separated by only a few tenths of a milliliter of alkali in strength comparable to that of the acid.

Alkali was titrated from a macro- (50 ml. capacity) buret until the solution was very close to the chitin end point. At that time, the flow was stopped as precisely as possible at a milliliter graduation mark, and the titration was shifted to a micro- (10 ml. capacity) buret. Alkali of the same concentration was added drop-wise from the latter until a faint turbidity indicated the chitin end point. Detection of this point was facilitated by utilizing the Tindall effect in a darkened room. Phenolphthalein was then added, and the drop-wise titration was continued to the acid end point.

RESULTS

The Chitin Spectrum

Aqueous acid solutions of chitin were placed in a thermostatic bath at 25°C. for one week, and daily observations of the spectrum were made upon samples taken from them. Figure 1 shows the type of spectrum obtained under these conditions, using distilled water and the acid solvent, respectively, as absorption standard. It will be noted that, whereas the spectrum based on the acid standard displays a regular rise in absorption as the wave length of the light decreases, that based on the water standard exhibits an irregularity at a wave length of about 240 millimicrons. It will be further noted that this irregularity becomes more and more prominent as the concentration of chitin decreases.

In order to establish the cause of this small discrepancy, qualitative spectra were determined under a variety of conditions. Study of the acid solvent against

a water standard demonstrated that the irregularity persisted even in the absence of chitin; hence, it must be due to the acid. Observation of the spectrum of sodium chloride against the water standard showed that it was no longer present, so eliminating the chloride ion as its cause. Further observations on hydrobromic

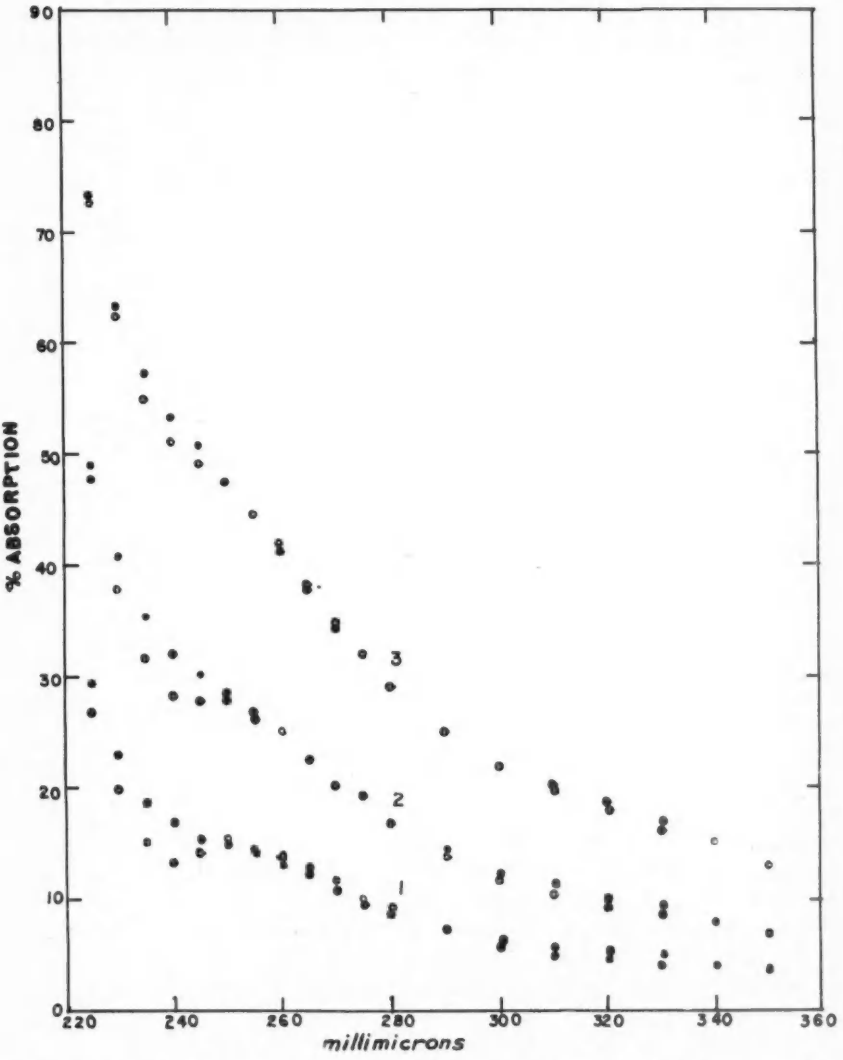

FIGURE 1. The ultraviolet absorption spectra of chitin in 0.0886 M HCl. Symbols: ○ = values based on a distilled water standard; ● = on HCl standard. Curve 1, 0.503; curve 2, 1.006; curve 3, 2.013 g. per liter.

and sulfuric acids showed it to be present in each case. It was therefore concluded that the effect must be attributable to the hydronium ion.

Now, the manner in which the magnitude of the irregularity varies with concentration of chitin shows that the hydronium ion is engaged in the formation of a complex with the chitin molecule. It is well known that the nitrogen atom has a strong tendency to add protons, and it seems probable that the nitrogen atom of the repeating unit in chitin is the point at which the complexing action occurs.

Effects of Hydrolysis on the Spectrum

It has long been known (3) that chitin can be hydrolysed in hydrochloric acid to give glucosamine hydyrochloride. Irvine reports that in strong acid this occurs in eight to ten hours at 40-45°C. While it is doubtful that any appreciable hydrolysis will occur at that temperature in solutions as dilute in acid as those studied here, nevertheless, the same solutions whose spectra are reported in Figure 1 were subsequently placed in a bath at 45°C. for one week, and daily observations of the spectrum were recorded. It was found that there were no significant changes over the period. Hydrolysis has no effect in the present system, if indeed it occurs at all.[2]

The Basicity Constant

In order to gain some idea of the magnitude of the basic effect of the nitrogen atom, it was thought that data like those of Figure 1 might be used in order to establish at least the order of magnitude of the apparent basicity constant. To this end, the acid-base equilibrium involving chitin can be set up as follows:

$$ChH^+ + H_20 \rightleftharpoons Ch + H_30^+ \qquad (1)$$

in which Ch represents the acetylglucosamine repeating unit, and ChH^+ represents the proton adduct of that unit. This adduct, we shall term the "chitonium" complex, or ion. From this expression, the apparent equilibrium constant for the acidity of the chitonium ion may be set up:

$$K_a \rightleftharpoons (H_30^+)\,(Ch)/(ChH^+). \qquad (2)$$

It was then assumed that, since the chitin spectrum vs. the acid standard follows Beer's Law, the irregularity in the simple acid solutions does also. If this be true, then the concentration of hydronium ion in equilibrium with the chitonium ion can be approximately determined by the difference between the curves based on the water and the acid standards, and the concentrations of Ch units and the chitonium, respectively, can be obtained from this quantity and the known original concentrations by stoichiometry. Reasoning upon this basis, apparent acidity constants were calculated for four different concentrations of chitin. The results are shown in Table I.

[2]Later experiments on the spectrum of glucosamine hydrochloride itself strongly tend to confirm the conclusion that no significant hydrolysis occurred here. The latter spectra are very different and will be reported at a later date.

TABLE I. Apparent acidity constants from spectral data.

Original concentration of chitin, *g./l.*	K_a
0.252	0.28
0.503	0.37
1.006	0.58
2.013	0.46
	Mean– 0.42 ± 0.098

As was to be expected from the nature of the calculations, the value obtained for the constant is of extremely poor precision. However, it does indicate the basic equilibrium constant is approximately 10^{-14}, as obtained through the well known relation.

$$K_b \rightleftharpoons K_w/K_a \qquad (3)$$

where K_w is the ion product constant for water at 25°C.

The titrations described in the experimental section were then undertaken as a means of establishing somewhat more precisely the values of K_a and K_b in the acid-chitin system. These measurements were based upon the hypothesis (qualitatively supported by the observation that, near the chitin end point, the chitin comes out of solution rather slowly, as well as by the fact that, in very weakly acid solutions, chitin dissolves at an immeasurably slow rate) that so long as there is an appreciable excess of hydronium ions present, the equilibrium concentration of chitonium ions will be temporarily maintained. That is to say, it was supposed that the rate of proton transfer (eq. 1) is very slow.[3] Hence, titration to the chitin end point yields the concentration of free hydronium ions present in the system, while titration from the chitin to the acid end point indicates directly the concentration of chitonium ions. The concentration of free chitin repeating units is obtained by difference.

From the data determined in this way, acidity constants were calculated from equation (2) for nineteen samples at four different chitin concentrations. These results are presented in Table II.

TABLE II. Apparent acidity constants as determined by titration.

Original chitin concentration, *g./l.*	Number of determinations	K_a	Mean deviation
0.4936	7	0.450	0.019
1.0208	3	0.442	0.002
1.5006	4	0.427	0.032
2.008	5	0.422	0.015
Mean	19	0.435	0.018

[3]This presumption requires further detailed investigation.

Invoking equation (3), K_b for chitonium is thus 2.8×10^{-14}, if we utilize the value of $K_w = 1.2 \times 10^{-14}$. It will be observed that the precision of the titration method represents a very considerable improvement over that of the spectral method. If the mean deviation may be taken as a measure of precision, the error is about 4.15 per cent of the quantity determined. If the median deviation (probable error) is used as a measure, the precision is somewhat better.

DISCUSSION

With regard to the spectra determined, there is little to be said apart from the interesting effect noted because of the formation of the chitonium complex. When the acid standard is employed, the absorption curve is quite featureless, the absorption depending only on the wave length and the concentration in the same regular manner reported by Merker(5). This indicates chiefly that the spectrum is unaffected by the degree of dispersion of the chitin molecules, as is doubtless to be expected. It also indicates that any possible hydrolysis which may have occurred in the preparation of the material has no influence on the spectrum.

Concerning the problem of the basicity constant, however, one may draw some interesting conclusions. Table III presents a comparison of K_b for chitin with the K_b's for some compounds more or less closely related to the chitin repeating unit. Aside from the new value for chitin, the data are taken from Lange's tables(4).

TABLE III. A comparison of the basicity constants for chitin with those for some slightly related compounds.

Compound	K_b
Acetamide	3.1×10^{-15}
Acetanilide	4.1×10^{-14}
Chitin	2.8×10^{-14}
Aniline	4.6×10^{-10}

To assess this comparison, it is necessary to recall the structural features of the compounds in question. These are well known, with the exception of that for chitin which for many years was not well established. However, in 1931, Bergmann and co-workers(1) did establish that chitin is a polymer of cyclic glucosamine units, the nitrogen being in the number two position and having appended to it one acetyl group. Hence, the chitin repeating unit may be regarded as a sort of "secondary amine", one substituent of which is a polymeric molecule.

Thus, with respect to structure, the nearest analogue to chitin in Table III is acetanilide. The analogy is not exact, since in acetanilide the nitrogen is attached to an aromatic ring, while in chitin it is bound to a saturated pyranose ring. However, it is interesting to notice that both these substances seem to be

about ten-fold better bases than acetamide, which has no aromatic ring. As a consequence, it appears that the resonant effect (in acetanilide) and the inductive effect of the pyranose oxygens (in chitin) have about the same order of influence on the basicity of the nitrogen atom.

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A Study of the Proteolytic Enzyme Activity of the Pyloric Caeca of Redfish[1]

By Joseph A. Stern and Ernest E. Lockhart
Massachusetts Institute of Technology, Cambridge, Mass.

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ABSTRACT

The proteolytic activity of an enzyme preparation from the pyloric caeca of redfish (*Sebastes marinus*) was studied and measured colorimetrically by the biuret reaction. The optimum temperature of this preparation was found to be 51-52°C. A statistical study of the data showed the optimum pH to be 8.75, or slightly higher than the optimum pH of trypsin. A comparison of the actions of a commercial leather bate, hog intestinal mucosa, papain, pancreatin, trypsin and the caecal enzyme of redfish on casein led to the conclusion that the pyloric caeca of redfish would furnish a suitable material from which to prepare a leather bate.

INTRODUCTION

The present state of the fish-processing industry on the Atlantic coast is so severely competitive that the processors are continually looking for new outlets for their waste materials. One use of fish waste that has shown considerable promise in recent investigations is the substitution of the pyloric caeca of various species of fish for hog pancreas as a source of enzymes in leather-bate preparations. These caeca are a number of blind finger-like sacs attached near the pyloric end of the stomach, and serve in a capacity somewhat similar to that of the pancreas of mammals.

In 1937, Johnston began an investigation on the use of pyloric caeca of certain species of fish as a source of tryptic enzymes for use in commercial bates. Comparing a cod pyloric caecal preparation with hog pancreas and a commercial bate, Johnston concluded that, in so far as the proteolytic and lipolytic enzymes are concerned, the pyloric caeca of cod would furnish a suitable material from which to prepare a leather bate. He also found that the proteolytic enzymes of the pyloric caeca of cod had a maximum activity at approximately the same pH as trypsin. He reported, at this date, that a dried preparation of the pyloric caeca showed the presence of a lipase and a low peptic and rennet activity but no amolytic activity.

In 1941, Johnston examined the various organs of cod, haddock, hake and mackerel, and showed that only the pyloric caeca and the intestinal mucosa of these fish offered possibilities as sources of commercial leather bates. He concluded that the proportion of enzymic constituents in crude preparations of cod caeca, cod intestine and hog pancreas are similar.

[1]Contribution No. 148 from the Department of Food Technology, Massachusetts Institute of Technology.

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Cooke and Chowdhury (1948) investigated the use of the pyloric caeca of spring, pink, sockeye and chum salmons as a source of tryptic enzymes. They observed that the behaviour of these enzymes was in many respects similar to that of enzymes occurring in mammalian pancreas and concluded that these enzymes could be used industrially for leather bating. Cunningham and Shuttleworth (1950) investigated the waste visceral residues from fish obtainable in South African waters, with the object of developing a wood-meal enzyme from the gut of such fish for bating purposes. They showed that under practical bating conditions no difference existed in bating action between the experimental bate and a commercial bate when the initial concentrations were adjusted to give equivalent gelatin liquefying potency and the same relative proportions of ammonium salts were present.

Redfish (*Sebastes marinus*) is of prime commercial importance to the New England fishing industry, with landings annually in the hundreds of millions of pounds. In addition, it is one of the few species of fish caught off the New England coast throughout the year. Therefore, it was proposed that an investigation be made of the possible use of redfish caeca in commercial leather-bate preparations.

This paper deals with the evaluation of the caeca as a source of proteolytic enzymes by comparison with a commercial bate and various other enzyme preparations, on a standard basis, and the determination of some of the kinetics of the crude enzyme preparation. The economics of the recovery of the caeca and of the preparation of an actual bate are not discussed.

METHODS

Preparation of Enzyme Extract

Pyloric caeca were removed from redfish (*Sebastes marinus*) fillet waste and immediately frozen by "dry ice". The fish had been caught 14 days previously but were in good condition, owing to excellent icing facilities aboard the ship and the low ambient temperatures. The dried caecal extract was prepared according to Johnston (1941).

The yield obtained from 16 kilograms of redfish fillet waste was 36.5 grams of the dried extract.

Preparation of Enzyme Solution

The enzyme solution was prepared by adding to 1.00 gram of the dried extracted caecal material 100.0 ml. of distilled water, shaking vigorously for about one minute and allowing the suspension to stand at 40°F. (4.40°C.) until equilibrium had been established in the solution. The period was experimentally determined to be of 6 hours' duration.

Preparation of Casein Substrate

Wilson (1928) described an elaborate procedure for the evaluation of a bate using elastin, collagen, keratose, casein and olive oil as substrates. Johnston (1937) evaluated his caecal preparations according to the methods described

by Wilson. Cooke and Chowdhury (1948), on the other hand, used only casein as a substrate throughout their investigation. Tauber (1949) also described a method for the estimation of bates in which casein was used as the substrate. Inasmuch as casein is the substrate prescribed in standard industrial procedures for the evaluation of bates, it was the only substrate used in the study presented here.

Two methods were employed in the preparation of solutions of casein. These were:

(*a*) A 2.5-gram amount of casein was dissolved in 100.0 ml. of appropriate phosphate buffer solution. Solutions so prepared were used in the preparation of the standard curve and in determining the influence of temperature on the digestion.

(*b*) Five-tenths (0.50) of a gram of casein was dissolved in 30.0 ml. of appropriate borate buffer solution. Solutions so prepared were used in the determination of the influence of pH on the digestion and in the comparison of proteolytic activities of the caecal extract with those of various other enzyme preparations.

The buffer solutions were prepared according to the methods of Peters and Van Slyke (1932), and Gortner (1938).

Measurement of Enzyme Activity

The method of measuring the degree of activity of the enzyme preparation was based on a colorimetric determination of the undigested protein material at the end of the reaction. The method used was a modification of the one described by Robinson and Hogden (1940), and Kingsley (1939, 1940) for the determination of serum total protein by the biuret reaction. The method differs from most methods previously reported in the literature for enzyme work in that it measures colorimetrically the amount of protein insoluble in trichloracetic acid following digestion, rather than the amount of protein soluble in trichloracetic acid at the end of the digestion.

An aliquot of the digestion mixture was removed from the digestion vessel and run into a 15-ml. centrifuge tube containing 6.0 ml. of a 10 per cent trichloracetic acid solution. The tube was then capped and placed in a water bath maintained at 80°C. for 10 minutes. The tube was allowed to cool, the cap removed and three drops of a wetting agent were added. The tube was recapped and centrifuged for 10 minutes at 1,800 rpm. The supernatant was removed by decantation and the tube drained for several minutes. One small drop of 3 per cent sodium hydroxide was added and the precipitated protein stirred into a paste. One-half (0.50 ml.) of the 3 per cent sodium hydroxide was then added and the paste completely dissolved. Eleven ml. of the hydroxide solution was added, followed by 0.30 ml. of a 20 per cent solution of copper sulphate ($CuSO_4.5H_2O$). The tube was then stoppered with a clean rubber stopper and shaken vigorously for one minute. Ten minutes later the mixture was centrifuged for 15 minutes at 1,800 rpm. Ten ml. of the supernatant liquid was transferred by pipette to a colorimeter tube and the optical density was measured in an Evelyn Colorimeter using a filter with maximum absorption at 540 mμ. The blank tube contained the 3 per cent sodium hydroxide solution.

The standard curve was prepared by taking 1.50-ml. aliquots of several concentrations of casein in phosphate buffer at a pH of 8.22 and carrying these aliquots through the procedure described above. Since the number of milligrams of protein per ml. of solution was known, it was possible to plot a curve of optical density versus milligrams of insoluble protein. Figure 1 is a sample standard curve plotted from data obtained in this manner.

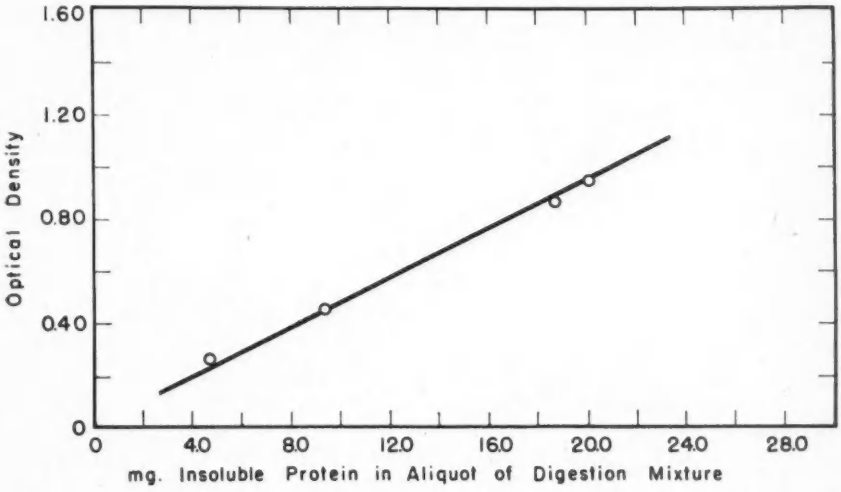

FIGURE 1. Sample standard curve for the determination of insoluble protein by the biuret reaction. Each point represents the average of three separate determinations.

EXPERIMENTAL

INFLUENCE OF TEMPERATURE ON DIGESTION

The influence of temperature on the rate of digestion was studied in the following manner:

Five (5.00) ml. of the clear supernatant enzyme solution was added to the digestion vessel containing 2.50 ml. of distilled water and 5.00 ml. of the casein solution. The digestion mixture, pH 7.92, was kept at the temperature selected, either in a water bath or in a hot-air oven, for one hour. During this period 2.00-ml. samples were removed at the end of 0, 12, 24, 36, 48 and 60 minutes, transferred immediately to 15-ml. centrifuge tubes containing 6.0 ml. of the 10 per cent trichloracetic acid solution, and analysed for insoluble protein.

The results, which indicated that the reaction was monomolecular (first order), were plotted on semi-logarithmic paper (logarithm of mg. insoluble protein versus time in minutes). The slopes of the plotted lines represented the velocities of the reaction at the various temperatures studied. Figure 2 is a graph of the relationship between slope values (equal to the velocities of reaction) and temperatures. The optimum reaction temperature as shown in this figure is 51°–52°C.

This optimum temperature seems high compared with values for the optima of animal enzymes generally found in the literature. It seems extremely high when one considers that *in vivo* the enzymes of fish must function at low temperatures. However, Sizer (1943) has stated that the optimum temperature of an enzyme reaction is not necessarily a function of the enzyme alone but is a function of the reaction under consideration, i.e. the enzyme-substrate ratio and the pH of the reaction. This may be an explanation for the high *in vitro* optimum temperature, since it is impossible to duplicate the natural conditions for the enzyme reaction.

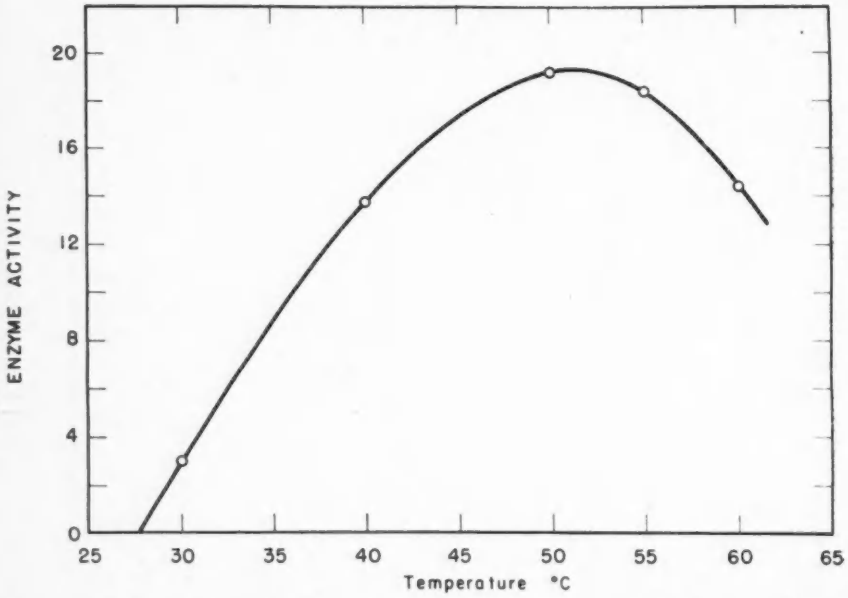

FIGURE 2. Curve illustrating the effect of temperature on the enzyme activity of the dried caeca of redfish when digesting casein in a buffered solution of pH 7.92.

The optimum temperature for the digestion of casein by prepared redfish caeca (51°-52°C.) seems to be fairly well correlated with those temperatures reported in the literature for caecal preparations from other species of fish. Cooke and Chowdhury (1948) reported the optimum temperature for the dried caeca of chum salmon, when digesting casein, to be 43°C., and Johnston (1937) reported the optimum temperature for the dried caeca of cod, when digesting casein, to be 45°C. However, Johnston (1937) also reported that Strather and Machon, in 1931, prepared an enzyme preparation from fish intestines with an optimum temperature of 55°C.

Influence of pH on Digestion

The influence of pH on the rate of digestion was measured in the following manner:

Five (5.00) ml. of the clear supernatant enzyme solution was added to a digestion vessel containing 7.50 ml. of the casein solution. The mixture was incubated at 50° ± 1°C. in a hot-air oven for one-half hour. At the end of this time, 2.00-ml. samples were immediately transferred to 15-ml. centrifuge tubes, each containing 6.0 ml. of the 10 per cent trichloracetic acid solution, and analysed for insoluble protein.

The data were analysed by the "Method of Least Squares" and the "best" quadratic curve of enzyme activity (Y) versus pH (X) was found to be:

$$\log Y = -10.90 + 2.77X - 0.1585X^2$$

The derivative of this equation was set equal to 0, and the optimum pH was calculated as follows:

$$\log Y = a + bX + cX^2$$

$$\frac{d \log Y}{d X} = b + 2cX = 0$$

$$\text{Then } X = -\frac{b}{2c} = -\frac{2.77}{2(-0.1585)} = 8.75$$

The curve derived above was then tested for significance by the "F test", as described by Freeman (1942). "F" was found to be 177 and the curve to be highly significant (99 per cent probability).

The experimental points that were obtained and the mathematical curve derived above are shown in Figure 3.

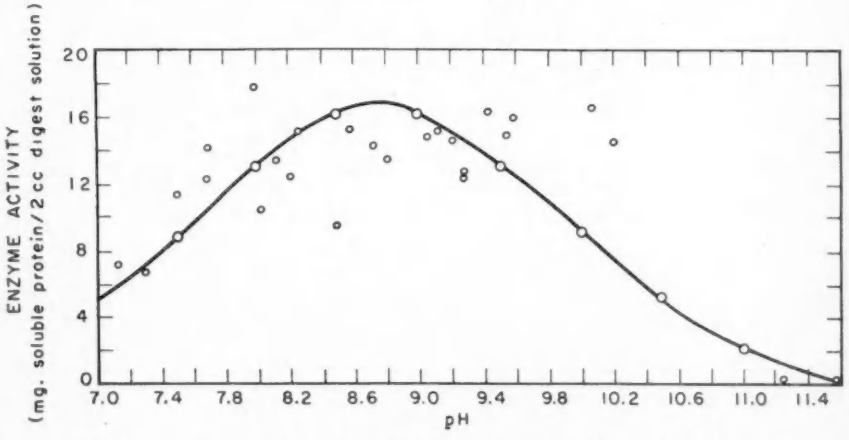

Figure 3. Superposition of the mathematical curve determined by statistical means on the scatter diagram of enzyme activity of the dried caeca of redfish across the pH range 7.00 to 11.6, when digesting casein at a temperature of 50° ± 1°C.

Johnston (1937), using a carbonate-borate buffer, reported the optimum pH for dried cod caeca when digesting casein to be about 8.5. Cooke and Chowdhury (1948), using a carbonate-borate buffer, reported an optimum pH of 8.3 for dried spring and pink salmon caeca, 8.5 for dried sockeye salmon caeca and 8.1 for dried chum salmon caeca when digesting casein. In other words, all the literature values reported on this subject and the value found in this investigation for dried redfish caeca closely correspond to the optimum pH (8.3) for mammalian trypsin when digesting casein.

Autolysis of Enzyme Solution

In all the computations in this present investigation, the amounts of enzyme precipitated as insoluble protein in trichloracetic acid solution were neglected. The reasons for this are: (1) it was assumed that the amounts of enzyme present in the digestion mixtures were uniform and, therefore, that equivalent amounts of enzyme were present as insoluble protein in all centrifuge tubes, and (2) it was determined experimentally that the amount of enzyme autolysed was negligible and independent of temperature and hydrogen-ion concentration during the digestion period.

Comparison of Proteolytic Activity of Caecal Preparation with Proteolytic Activities of Several Enzyme Preparations

The activities of the various enzyme preparations were measured in the following manner:

One-gram quantities of papain, hog intestinal mucosa, pancreatin, trypsin, a commercial leather bate and the caecal extract were suspended in distilled water, each amount separately in 100.0 ml. The suspensions were shaken vigorously for about one minute and then incubated at 37.5°C. for 15 minutes. Five-(5.00) ml. amounts of clear supernatant liquid from the several suspensions were added to separate digestion vessels, each containing 7.50 ml. of casein solution at a pH of 8.40. These mixtures were held at 40° ± 1°C. in a hot-air oven for one-half hour. At the end of this time, 2.00-ml. aliquots were transferred from the digestion flasks to 15-ml. centrifuge tubes, each containing 6.0 ml. of the 10 per cent trichloracetic acid solution. The aliquots were then carried through the procedure described above for the measurement of enzyme activity. A blank for each enzyme solution was carried through the digestion and assay procedures.

The data obtained from this experiment are presented in Figure 4.

If the activity of trypsin is taken arbitrarily as 100, the relative activities of the other preparations are as follows: pancreatin, 95; dried redfish caeca, 77; papain, 32; commercial bate, 13; and hog intestinal mucosa, 10. As the caecal preparation might be diluted seven times with a filler and still yield a bate having an activity comparable to that of the commercial bate tested, it appears reasonable to state that redfish pyloric caeca are a potential source of commercial bates.

The economics of the production of a caecal bate have not been studied. However, the results reported here seem to be in general agreement with those of Cunningham and Shuttleworth (1950), who stated that 3 pounds

of viscera when dried with 1 pound of woodmeal would yield 1½ pounds of product, which in turn could be used to produce 3 to 15 pounds of commercial bate.

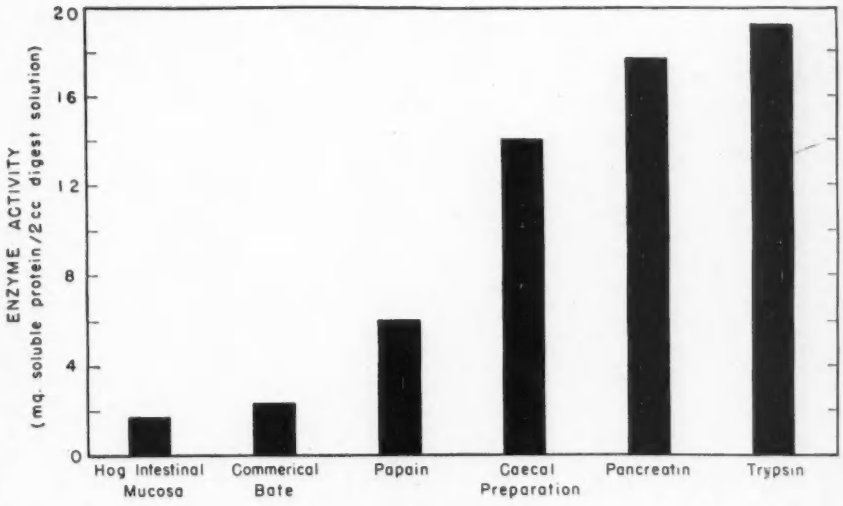

FIGURE 4. Histogram comparing the activity of the dried caeca of redfish with a commercial leather bate and other enzyme preparations when digesting casein in a buffered solution of pH 8.40 and at a temperature of 40° ± 1°C.

SUMMARY

The proteolytic activity of the enzymes of the pyloric caeca of redfish (*Sebastes marinus*) was studied and measured colorimetrically by the biuret reaction.

When casein was used as a substrate, the optimum temperature for proteolytic activity was found to be 51°- 52°C. With the same substrate and at 50°C. the optimum hydrogen-ion concentration for proteolytic activity was found to be 1.778×10^{-9} (pH=8.75).

A comparison of the proteolytic activities of a commercial bate, hog intestinal mucosa, papain, pancreatin, trypsin and the enzymes of the pyloric caeca indicated that the pyloric caeca of redfish would furnish a suitable material from which to prepare a leather bate.

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